

# Fossil flies in Baltic amber – insights in the diversity of Tertiary Acalyptratae (Diptera, Schizophora), with new morphological characters and a key based on 1,000 collected inclusions

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**Abstract:** A review of specific publications dealing with Baltic amber Diptera, Acalyptratae, from the years 1822 until 2008 includes 38 articles. H. LOEW was the first entomologist searching systematically for Diptera in amber. Two of his three articles are discussed. Parts of his first one (1850) are translated from German because of its extreme rarity in libraries. From Eocene Baltic amber 35 families of acalyptates are known now, a further four from British Eocene sediments. Natalimyzidae, Piophilidae and Pyrgotidae are recorded for the first time, *Natalimyza* was known only from the recent Afrotropical fauna. Different counts of the percentage of acalyptates among insect-, Diptera- and “true fly”-inclusions, respectively, are compared. Less than 1% of all flies belong here. Reasons for this rarity are discussed together with an overview of the rare aggregation of acalyptates in single amber pieces. Peculiar morphological apomorphies, which enable family identification worldwide because of their singularity, were already present during the Tertiary. Three such examples are discussed. The dispute about the doubted synchronous genesis of German Bitterfeld amber is solved by demonstrating 15 conspecific acalyptate species in both deposits. Intraspecific variability of an amber acalyptate has never been studied before. On the basis of 45 specimens and the holotype of *Protoscinella electrica* (Chloropidae) the slowness of evolutionary transformations is exemplified with the background of the phylogenetic value of 16 selected characters. A spotlight is thrown on the polyphyletic reduction process in wing venation and bristle equipment observed in several families of acalyptates.

The systematic part presents overviews of a large number of morphological details used for taxonomy. Two tables enable the easy check and documentation of each detected specimen, as well as an understanding of the puzzling termini and abbreviation systems in subsequent periods of dipterology. Two differently organized identification keys are presented: one listing 97 exceptional, rare, or newly detected morphological peculiarities, a second one is a trial to key out all 56 described and all 161 detected undescribed species. The well known terminology of HENNIG's publication series on amber is used in order to enable an easy cross-reference to his partly complicated descriptions, to his plenty of figures, and to the dipterous literature until the year 1981 when a new terminology was proposed. All family- and generic transfers since HENNIG's times are listed with their references, as well a species breakdown of parts of the identified 1,141 inclusions.

**Key words:** Apomorphies, Bitterfeld amber, Calyptratae, chaetotaxy, Chloropidae, Pyrgotidae, speciation, variability.

**Santrauka:** 1822-2008 metais paskelbtos 38 moksliškės publikacijos, skirtos Baltijos gintare rastiems Diptera, Acalyptratae vabzdžiams. H. LOEWAS buvo pirmasis entomologas, sistematiskai tyrinėjės dvisparnius gintare. Aptariami du iš trių jo straipsnių. Atskirojo jo pirmojo darbo (1850) dalys yra išverstos iš vokiečių kalbos, nes publikacija yra tapusi didele bibliografine retenybe. Iš eoceninio Baltijos gintaro dabartiniu metu žinomas 35 akaliptratiniai dvisparniai (Acalyptratae) šeimoms. Dar trys rastos eoceninėse nuogulose Didžiojoje Britanijoje. Agromyzidae, Natalimyzidae, Piophilidae, Pyrgotidae ir Sphaeroceridae yra aprašomos pirma kartą, *Natalimyza* buvo žinoma tik iš dabartinės Afrikos tropikų faunos. Palyginami skirtingu autorių pateikiami akaliptratų gausumo paskaičiavimai tarp visų vabzdžių, dvisparnių ir “tikrujų musių” inkliuzų. Šioms musėms priklauso mažiau negu vienas procentas gintare randamų inkliuzų. Šio retumo priežastys aptariamos kartu apžvelgiant retai pasitaikančias akaliptratų sankupas viename dintaro gabale. Ypatingos ir kartu unikalios morfologinės apomorfijos, kuriomis pasižymi visos Žemės rutulyje sutinkamos akaliptratinės musės, egzistavo jau terciarie. Aptariami trys tokie pavyzdžiai. Diskusija apie abejotiną tą pačią vokiškojo Bitterfeldo ir Baltijos dintarų kilmę išsprendžiama parodant, kad abiejose dintaruose randama 15 vienodų Acalyptratae rūšių. Vidinis rūšinis variavimas tarp dintaruose randamų akaliptratų anksčiau nebuvu tirtas. Remiantis 45 pavyzdžiais ir *Protoscinella electrica* (Chloropidae) holotipu demonstruojamas evoliucinių transformacijų létumas kartu pagrindžiant 16 parinktų požymiu filogenetinių reikšmingumą. Nušviečiamas polifiletinis sparno gylslotumo ir šeriutumo redukcijos procesas, stebimas keliose akaliptratu šeimose.

Sistematikai skirtoje dalyje aptariama daug taksonomijai būdingų morfologinių požymiu. Pridedamos dvi lentelės, labai palengvinančios kiekvieno rasto egzemplioriaus patikrinimą ir dokumentavimą bei padedančios suprasti klaidžias terminologijos ir trumpių sistemų, naudotas dipterologijoje skirtingais periodais. Darbe pateikiami du skirtinti apibūdinimo raktais: viename išvardijami 97 išskirtiniai ar reti naujai pastebėti morfologiniai ypatumai, antrame bandoma apibūdinti 56 aprašytas ir 161 rastas, bet neaprašytas rūšis. Vartojama gerai žinoma HENNIG'o gintarui skirtų publikacijų serijos terminologija. Tai daroma norint palengvinti šių gana sudėtingų aprašymų ir gausių iliustracijų bei dipterologinės literatūros, išspausdintos iki 1981 m., kada buvo pasiūlyta nauja terminologija, analizę. Visi rūšių perkėlimai iš vienų šeimų ar genčių į kitas, atlikti po HENNIG'o laiką, išvardijami pateikiant publikacijų nuorodas. Taip pat pateikiami rūšių "suskaldymai", kurie įvyko ištystus 1141 inkliuzas.

**Raktiniai žodžiai:** apomorfijos, Biterfeldo gintaras, Calyptatae, Chloropidae, Pyrgotidae, rūsių susidarymas, variabilumas.

## Introduction

Since the opening of the Iron Curtain 20 years ago studies on amber insects underwent a new revival. Groups of amber friends were established, amber dealers learnt to identify the insect orders and families, and they travelled around in order to present their stones to museums and private collectors. The authors of this article benefited from this boom and brought together a special collection of Acalyptratae, a group of almost tiny flies, which were rarely selected from amber. Amber acalyptates had been identified in the past by some few specialists only, most notably the world foremost authority, Willi HENNIG. In a series of papers (1940, 1965, 1966, 1967, 1969, 1971, 1972) he published comprehensive and detailed research on the Baltic amber acalyptates including a revision of MEUNIER's descriptions around hundred years ago. For the determination of half a hundred species he really had to rack his brain. He worked up the material of European and North American collections in museums and palaeontological institutes. HENNIG examined 124 specimens, which he classified in 30 families and 49 species out of which 39 were described as new. More than 300 printed pages offer us a vast array of phylogenetic speculations accompanied by excellent figures. HENNIG himself spoke of situations in which certain inclusions exasperated him. The reader, not well understanding his complicated German\*, may just as much been despaired in getting a clear picture of his results. Surely that was one of the reasons that the subject was neglected after his death.

Since HENNIG's last paper in 1973 just seven erratic descriptions of Baltic amber acalyptates were published though the flood of amber publications swelled up rapidly. Dirk TEUBER (Gütersloh), collector of amber literature, altogether catalogued 3,306 books and articles for the years 1550 till 2006. The increase of amber publications, step by step, over the last five decades since 1956 was as follows: 84, 104 (including 1976, the year of HENNIG's death), 242, 729, and 1,233 (including 2006) (pers. comm.), an impressive disproportion to the mere 18 publications (cited below) since 1976 dealing at least in a short part with some amber acalyptates out of the large number of families.

## Material and methods

The optical observation of acalyprate inclusions is a complicated procedure influenced by the amber matrix itself and by the condition of their preservation. Inclusions embedded in transparent amber without impurities are quite rare, their morphological characters are as easy to observe in such a piece as in extant fly specimens. In most cases, however, important structures can be obscured by crust of the amber surface, cracks, fissures, gas bubbles, mineralic precipitations like pyrite, plant debris or syn-inclusions. If an inclusion is situated directly beneath or nearby an opaque layer of resin it is only visible from one side.

A typical phenomenon of Baltic amber inclusions is a milky coating (German term: Phloem, Verlumung) interpreted often as "mould" but caused by microscopic, liquid-filled bubbles, almost only on one side of the insect (presumably influenced by sun exposure during the embedding and following rotting process). This covering can obscure the embedded objects partially or totally. In other cases the black insect bristles penetrate this coating and are better visible than on shiny dark surfaces. Another problem is a technical process used in the amber industry in order to clear opaque amber samples in a so-called "autoclave". Amber inclusions, which were treated in a high-temperature autoclave, are mostly more or less deformed, compressed and dark-brown to almost black, looking "cooked". The integument of the body is more or less shrunk and bristles may have lost their connection to the original point of insertion. Measurements of such fossils are unreliable (see also SZWEDO & SONTAG 2009).

The very first step before our analysis was processing the amber pieces: cutting, grinding and polishing as close and as parallel as possible to the frontal, dorsal and lateral sides of the fly. Oblique views were occasionally unavoidable if specimens were lying too close to the surface of a round stone. Subsequent embedding in artificial resin, followed by renewed grinding and polishing, can eliminate a convex or concave surface of a stone, or it enables a perpendicular view on a wanted plain.

\* For an English translation see HENNIG 1965.

Moreover, such a procedure (always only after complete evaporation of all water in the fissures) protects fragile samples from breaking and weathering. Two-component polyester or epoxid resin, available in shops for craft supply, have a similar optical quality and refractivity as amber. Our labor-intensive procedure facilitated the stereoscopic investigation. All embedding should always be done only after a first thorough study of an inclusion in order to search for the most important structures for identification and correct grinding plains.

Scientists need a lot of time to focus on an inclusion and to detect all characters necessary for a careful analysis. If the main features, the chaetotaxy of head, thorax and legs are impossible to observe because of obscured characters, bad position or an incomplete specimen, an exact determination to genus or species, even to family level remains insufficient. But even such poorly preserved flies often become valuable when further specimens of the same species are detected later on, as we may use them for the study of singular additional details.

Altogether we investigated 1,141 individuals of acalyptates embedded in 1,063 stones, which (with the exception of seven) had not been used in foregoing studies. Some are insufficiently considered in the identification key as they are loaned to other dipterists in Europe and abroad since several years. The material belongs to the following collections: Museum of the Earth, Warszaw (1), Natural History Museum, London (1), Zoological Museum, Copenhagen (1), EICHMANN (24), GRÖHN (57), HOFFEINS (465), KERNEGGER (86), LUDWIG (13), TEUBER (2), VON TSCHIRNHAUS (491).

## Results

### Historical background – the earliest and the present times

A first description of four acalyprate fly inclusions in Baltic amber was presented by PRESL (Prague) in 1822 (an extremely rare book present in only one public library of Germany, Göttingen). The types are assumed to be lost and none of the "Musca"-species can be allocated to a valid taxon (HENNIG 1965). Before 1850 LOEW began to study the dipteran inclusions of his private collection and the large BERNDT-collection, which is housed at the "Paläontologisches Institut, Museum für Naturkunde" at the Humboldt University of Berlin since 1873. The LOEW-collection was purchased in 1922 by the British Museum of Natural History (now Natural History Museum) and is deposited in its Department of Palaeontology. Three articles on amber acalyptates were published by LOEW: 1850, 1861 and 1873.

Detailed descriptions of acalyprate inclusions were made by MEUNIER in six articles (1895, 1899, 1904,

1905 [new name for a homonymy by HENDEL 1923], 1908, 1917). They were mostly stored in the former collection of the Königsberg University, East Prussia. After World War II this collection was deposited at the "Geologisch-Paläontologisches Institut der Universität Göttingen". According to HENNIG (1965) most types described by MEUNIER are safely stored. All modern insights in the world of amber acalyptates were presented by HENNIG (1940, 1965, 1966, 1967, 1969, 1971, 1972, 1973). In those times the Conopidae still were placed outside the Acalyptratae, today it is presumed that they would best be placed near the Tephritidae. STUKE (see below) in his amber papers presents no opinion on this matter.

New genera and species were described as follows: STUKE (2003, 2005) two new Conopidae; HOFFEINS & RUNG (2005), one new Periscelididae; WOZNICA & PALACZYK (2005) and WOZNICA (2006, 2007) altogether three new Heleomyzidae; GRIMALDI (2008) one new Camillidae. All these taxa are included in the identification key below. Further studies, but without descriptions of new taxa, were published by D.K. MCALPINE (1966, Cypselosomatidae), MORGE (1967, Lonchaeidae and Pallopteridae), J.F. MCALPINE (1977, Proneottophilidae), J.F. MCALPINE (1981a, Pallopteridae), J.F. MCALPINE (1989, Clusiidae), SCHUMANN (1994, Diopsidae), WHEELER (1994, Carnidae), ROHÁČEK (1998, 2006, Anthomyzidae), HAENNI (2003, collection), and KOTRBA (2004, Diopsidae). EVENHUIS (1994) catalogued all known fossil Diptera of the world including compressions, impressions, trace fossils, copal, and amber.

### Hermann Loew and the acalyptates

The second scientist who detected acalyprate flies in amber was LOEW (1850). OSTEN SACKEN (1903-4, reprint 1978), in his classical book on his life in entomology, wrote 24 interesting pages on the character and career of his colleague Hermann LOEW including also a long chapter on his work on amber, which was never finished. Nevertheless, OSTEN SACKEN after his long intercourse with LOEW "threw some light on this otherwise very obscure subject". Also, in 1864, he made LOEW's second amber article available in the English language, which was originally published in a journal not easy to obtain today (LOEW 1861; OSTEN-SACKEN 1864). LOEW himself wrote in a letter: "Minutiae are my true speciality, particularly when they fall within the domain of the Acalyptrata!" His first sentences on amber Acalyptratae (l. c.) never were translated. As they were published in a nearly inaccessible "journal", a school programme of the gymnasium where he was the director, we cite him here in our translation:

**"Fam. 21. Myopina.** The Myopina contain only one most curious species, which seems to require the description of a new genus; it equals more a *Myopa* than a *Conops*, but it definitely misses the swollen head shape of *Myopa*-species, moreover it has a quite short and thick proboscis like that to be found also among extant species of the genus *Conops*. " It follows "**Fam. 22. Muscaria**" (see below) and "**Fam. 23. [sic!] Anthomyina**" (without any mentioned genus) continued by:

**"Fam. 23. Acalyptera.** I understand this family in that extent as MEIGEN interprets the *Acalypterae* in the 7<sup>th</sup> part of his publication, but I exclude all those genera, which distinguish themselves by a variant habitus. Out of the 28 species belonging here, only very few can be determined up to genus level. Most of them belong to the extremely doubtful objects. But I believe to have recognized with certainty the genera *Sapromyza*, *Helomyza*, *Ephydria*, *Drosophila* and *Chlorops*. – These and the two families mentioned above (Fam. 21. Myopina, Fam. 22. Muscaria) include a large and interesting part of the system: in spite of the richness of the material, which passed my hands, I can contribute only poor information. It may be explained by the fact that among 200 amber flies hardly more than one can be found, which belongs to the relationship of these three families. Collectors will render a special merit, if they pay attention to this group of related Diptera."

**"Fam. 24. Leptopodea.** I detected two nice *Calobatta*-species, which belong to this family, which can be distinguished so easily; the body size of one specimen equals that of the longest exotic species."

As "Fam. 22. Muscaria" LOEW (1850) records 12-14 seen specimens of Calyptratae, families Muscidae, Anthomyiidae, Sarcophagidae, and Tachinidae. He could not order any of them to one of the three mentioned families, which to this day are all still unknown from Baltic amber. Only one specimen of Anthomyiidae is known to date (MICHELSEN 2000). But one of us, M.v.T., possesses one female of a poorly preserved ?Tachinidae with 9 larvae behind its ovipositor. Also H.-P. TSCHORSNIG, specialist for this family, was not able to confirm a reliable family identification. In Dominican amber, too, these most "modern" larger flies are extreme rarities, four species were only described to date (MICHELSEN 1996; PONT & CARVALHO 1997). Probably larger flies were powerful and quick enough to escape the sticky resin. Families which could be confirmed by later authors had already been recorded by LOEW as "undoubtful" inclusions in the following sequence (modern taxonomy): Diopsidae, Conopidae, Heleomyzidae, Drosophilidae, Chloropidae, and Micropezidae. Though we studied much more material than ever before we could not confirm any specimen of

Ephydriidae, a family with species not being abundant within shady forests but mainly living along freshwater shores and marine beaches or developing on open grassland as leaf-miners or snail-predators. (But several species of Parydrinae were identified by specialists of ephydriids from Dominican amber; pers. comm.). Surely LOEW mixed up ephydriids with Periscelididae or Aulacigastridae because of their similar fronto-orbital bristles and partly convex and prominent face. One further family, the snail-killing Sciomyzidae, was listed by LOEW as doubtful. After our collecting activities this family 160 years later is very well represented with several undescribed species. They are under study now by L. KNUTSON.

In his 1861 article LOEW added only one further undoubtful acalyprate family, the Diopsidae, and he expressed some ecological thoughts, exemplified by five species of Diptera: "The following species may be named as indicative that the climate of the Amber period was very probably somewhat, although not very much, warmer than the present climate of Prussia: ... 3. *Sphyracephala*, a close relative of *Sphyracephala brevicornis* SAY, common in the middle and southern of the United States, the only living representative of the genus as yet known. ..." (translation by OSTEN SACKEN 1864: 311). KOTRBA (2004) gathered all available 28 inclusions of *Prophyracephala succini* (LOEW) and lightened diopsid evolution in her cladistic analyse of morphometric measurements. In addition LOEW added some further doubtful acalyprates, mentioned here in the modern system: Lonchaeidae, Opomyzidae and Piophilidae. Last but not least, LOEW listed families which he said he undoubtedly never saw in amber: (in the modern system) Psilidae, Ulidiidae, Tephritidae, Sepsidae, Agromyzidae, Coelopidae, Asteiidae, and Sphaeroceridae. Out of these, Psilidae have been separated by us repeatedly, according to quantity followed by Pallopteridae. The families Sepsidae and Asteiidae still are absolute rarities, while the marine Coelopidae from marine shores (possibly LOEW's Phycodromidae were misidentified Dryomyzidae of which to date two fossil species are known) and Sphaeroceridae are unknown inclusions until today with two exceptions: HELM (1896: 223) mentioned two sphaerocerid specimens in his collection as "Borborus", and one of us (M.v.T.) saw one Baltic amber specimen of this family with its peculiar shortened hind metatarsi (= basitarsi) and the typical thin long arista. Unfortunately, this inclusion seems to have been mislaid or stolen in the Bielefeld University, nevertheless we included it in the key but omitted it from the other surveys. The absence of the last family remains an enigma as these flies are so abundant in extant nature. But their ecology (occurrence in moist hidden rotting substrates and leaf litter) is not in coin-

cidence with the abiotic conditions of sun exposed fresh amber droplets on twigs and trunks.

## Further Eocene Acalypratae

Recently ZLOBIN (2007) studied types and other fossil acalyprates described by COCKERELL from the "younger Lower Tertiary of the Hampshire basin (Bembridge Marls. 35 m.y. B.P.)", which had been ordered by EVENHUIS (1994) to the families Sphaeroceridae, Richardiidae, Ephyrinidae and Chloropidae. They were recognized by ZLOBIN as Anthomyzidae, Ephyrinidae, Chloropidae, Agromyzidae, Otitidae, Heleomyzidae, and Lauxaniidae. One of us (M.v.T.) has studied the type of *Protoscincus perparvus* COCKERELL, 1917 in the year 1994 and had identified and labelled it as an ephydrid, tribe Scatellini. The transfer was officially published now after ZLOBIN came to the same result, removing this taxon from the Chloropidae. Some dipterists are not content with some of the further transfers. They are mentioned here as European Tertiary acalyprates for the sake of completeness. In the same context one out of eleven articles on fossil mines of the larvae of leafminer flies (Agromyzidae) in trunks of Tertiary trees (SÜSS 1980) is cited here in order to demonstrate that our search for a possible worldwide first confirmed amber agromyzid did not reveal any adult fly. It is not understandable that just the only cambium/xylem miners among the order Diptera are absent in amber though today they are abundant in tropical forests (VON TSCHIRNHAUS 1991) and are as well occurring everywhere in northern temperate latitudes. Oak trees (*Quercus* spp.) are hosts of *Phytobia mallochi* (HENDEL, 1924) in Europe (VON TSCHIRNHAUS 1993: 480). But timber of the abundant oak trees in Baltic amber forests – stellate hairs of their flower buds are to be found in nearly each amber piece – seems not to have been attacked by *Phytobia*-flies or their ancestors.

## How many inclusion stones must be collected to find one member of Acalypratae?

LOEW's (1850) rough estimation of the percentage of acalyprates among all his identified flies, being one out of 200 (0.5%) ("... das[s] auf 200 Bernsteinfliegen schwerlich mehr als eine kommen wird"), suits the following compilation well: Three labour-intensive investigations on the abundance of Diptera have been published, which contain records on Acalypratae (HOFFEINS & HOFFEINS 2003; SONTAG 2003, 2004). Rareness is the common result.

Any statement concerning a frequency expressed as percentage seems more or less speculative because all inclusion collections in institutions as well as most in pri-

vate hands were purchased from multi-pre-selected material. Based on totally **unselected** material with special reference to Diptera the following results were obtained by HOFFEINS & HOFFEINS (2003) after the selection of 39 specimens of acalyprates:

among	17,119	insect inclusions:	0.22%
among	10,778	Diptera inclusions:	0.36%
among	2,125	Brachycera inclusions:	1.83%
among	1,351	Dolichopodidae inclusions:	2.88%

In a more general sense that means: in 2,000 brachyceran inclusions less than 2% were acalyprate Diptera and in about 1,350 inclusions selected as "family Dolichopodidae" ("long-legged flies", the most common dipteran family in amber) less than 3% were acalyprates. In the words of our experienced friend A. KRYLOV (Kalinigrad): among 1,000,000 unselected grinded stones "fresh" from the deposit, only **one** acalyprate inclusion may be picked out, out of all scientific useful inclusions 0.04%, while out of all Brachycera 0.5% are Acalypratae, 0.5% Syrphidae and Pipunculidae, and 2% are Rhagionidae, Tabanidae and Asilidae.

SONTAG (2003) selected from 3,875 checked stones 1,824 pieces containing zoo-inclusions: 4 acalyprate flies, all ?drosophilids, were obtained only:

among	7,111	animal inclusions:	0.0006%
among	4,933	insect inclusions:	0.0008%
among	2,947	Diptera inclusions:	0.0014%
among	402	Brachycera inclusions:	0.9950%

SONTAG (2004) identified all 6,096 Diptera inclusions in the Gdansk Amber Museum to the family level, which are 50% of all arthropods and 65% of all insects in the museum. Only 8 acalyprates were detected: 6 Drosophilidae, 1 Psilidae, and 1 Micropezidae, altogether 0.013% of all Diptera.

This short overview demonstrates the influence of different sampling and selecting methods. The differences of counting on the basis of all Diptera between HOFFEINS & HOFFEINS and SONTAG are 0.36% and 0.001%, respectively, that means the first authors detected 265 times more acalyprates among all Diptera than their Polish colleague! LOEW, HOFFEINS & HOFFEINS, and SONTAG counted 0.5%, 1.8% and 1.0% acalyprates, respectively, among all identified flies (Brachycera), an astonishingly similar result, which let us speculate that mainly the thorough counting of all Nematocera (midges and gnats) among the Diptera influenced the sums and percentages.

## Geological duration of the amber forests

We are not specialists for the question when the Baltic amber forests emerged and when they decreased.

We need this information for the next chapters, thus let us cite Wolfgang WEITSCHAT (2008: 94) in our translation of an article not easy to obtain for entomologists outside of Germany:

"The genesis of amber in northern Europe probably started already during the climatic optimum in the Lower Eocene and possibly was already finished towards the end of the Middle Eocene. As meanwhile confirmed the definite cooling of Northern Europe during the transition time Eocene/Oligocene caused an irreversible floristic change from palaeotropical towards arcto-Tertiary elements. A similar destiny might have affected fauna and flora of the 'amber forests'. This assumption is supported by the identity of organisms concerning the species-level of both deposits, especially of the tropical-faunistic and -floristic elements. This fact is now definitely documented by analysing the spider fauna. Baltic and Bitterfeld amber originate from one single 'amber forest' in western Scandinavia, which ranged over a period of up to 10 million years during a balanced subtropical-tropical climate ..."

## Diversity and Apomorphy

A recent updated counting of the diversity of Acalyptratae in Germany (VON TSCHIRNHAUS 2008) revealed 1,927 published species belonging to 51 families. Agromyzidae (leaf miner flies) were counted by 552 species, not including 102 additional undescribed species from Germany in the VON TSCHIRNHAUS-collection; some 170 valid further species are known from our directly adjoining neighbouring countries, altogether we await 724 species. The second place in extant diversity holds the Chloropidae, 198 published German species, followed by 177 Ephydriidae, 137 Sphaeroceridae, and 110 Tephritidae. Among these only the chloropids are regularly present in Baltic amber, *Protoscinella electrica*, and two rare species, *Protoscinella* sp.n. and *Tricimba* sp.n.; *P. electrica* is one of the most abundant acalyprate fly species in Baltic amber though only the holotype was known hitherto. (We can also state, that *Tricimba*-species belong to the dominant acalybrates in Dominican amber, which are all still undescribed). Three specimens of Sphaeroceridae are mentioned in the chapter on H. LOEW.

The three chloropid species possess all family-specific apomorphic characters also known from extant Chloropidae including two apomorphic features singular among all Diptera: a sharp perpendicular ridge along the propleuron and a small kink or flexure in the basal part of the  $m_{3+4}$ -vein which marks the junction point of a crossvein lost at least during the Cretaceous times or earlier. Such specific apomorphisms ("modern" characteristics) can be documented for most other families,

too. They provoke the question when in the dark past such peculiarities evolved and which were their provoking adaptations. Another example is the Clusiidae with their specific 2<sup>nd</sup> antennal segment bearing a triangular extension at outer surface lapping over onto the 3<sup>rd</sup> article. We cannot present any speculation about possible benefits of such a phylogenetically stable minute morphological detail.

Last but not least, we point out a third interesting example out of so many others: the first two species of fossil Pyrgotidae, which we detected in amber, of which one already possesses only one ocellus. Extant Pyrgotidae predominantly are dawn- or night-active tropical parasitoids of big scarabaeid beetles. Already in the Tertiary or earlier they had reduced two of the three ground-pattern ocelli, a process which seems still progressing. Extant forms predominantly reduced all ocelli but some still possess one or three or rudimentary ones. At least one of our species has very peculiar claws, not curved normally but bent over in an abrupt angle of 90°, never seen in other flies. These specialized claws seem to have been an adaptation to grasp glossy surfaces of beetles during nocturnal flight (as stated for extant species) for oviposition into their abdomen. They were already developed 45 million years ago! Similar to most recent species it is a large acalyprate in adaptation to the large size of its presumed hosts. Extant pyrgotids predominantly feature a singular character among the higher Diptera, the absence of a "mid-coxal prong", a soft but complicated structure above the mid-coxa of all other higher Diptera. We cite only one of several papers of the same authors dealing with the biomechanics of this structure: FRANTSEVICH & FRANTSEVICH (1999). In opposition to the statement in several manuals or handbooks of Diptera, one of us (M.v.T.) saw one Nearctic (*Pyrgota undata* WIEDEMANN) and some extant tropical pyrgotids still possessing the prong. One of our fossil species is so well embedded that we can document that the loss of the prong in some of the species of the pyrgotid family was already finished in the Tertiary. Another peculiar morphological detail in some extant pyrgotids is "hind tibia sometimes with basal third rather suddenly smaller in diameter than apical part (Fig. 6)" (STEYSKAL 1987). Just this can be observed in our fossil species. But different than the extant species the fossils still bear a dorsal preapical bristle (dpr), belonging to the groundpattern of acalybrates, at least on the hind tibia. The presence of these setae demonstrates that there was an ongoing evolutionary rudimentation process since the Tertiary.

## Intraspecific variation within millions of years exemplified by *Protoscinella electrica* (Chloropidae)

One example of morphological variability should be demonstrated: Producing our provisional key for the identification of fossil acalyptates embedded in resin over a period of estimated 10 million years (WEITSCHAT 2008) we came across the problem where the limits of a species definition should be drawn. It is well known that the velocity of speciation and morphological modifications is different in different animal groups. Extant species of millipedes (Diplopoda: *Polyxenus* LATREILLE, 1803, worldwide distribution) or exceptional spiders (Araneae: Archaeidae KOCH & BERENDT, 1854 with the fossil genus *Archaea* L., 1758 and three similar extant genera in Madagascar, South Africa and Australia) among the land living arthropods look quite equal to their fossil relatives preserved in Baltic amber. Their life strategies and ecological niches seem to have remained stable. In *Polyxenus* the predominantly parthenogenetic mode of reproduction in extant representatives may be presumed for the Tertiary only if more specimens (than we saw) turn out to be females. In palaeontology we can rarely find an object in which evolving minute structures, such as single bristles, can be studied as if the specimens were collected today. The variability within the evolving process of *Protoscinella electrica* (Chloropidae, Oscinellinae) over a period of millions of years can be compared with the interspecific variation of the sister genus *Tricimba* LIOY, 1864 differing only morphologically in the absence of setulae on the dorsal side of the subcosta vein. ISMAY (1993) published an impressive overview on the interspecific morphological variety of this genus in the zoogeographical region of Australasia, which is an example also for the *Tricimba*-species in other world regions including Europe. Compared with the succeeding extensive splitting in chloropid systematics ISMAY's concept of the judgement of morphological details (judged as not being important enough for a splitting of this genus) is welcome.

Altogether 45 inclusions (subsequently called "series") of *P. electrica* could be studied, including the ♀-holotype from the Copenhagen Museum, 1♂ from the London Natural History Museum, 3♂♂ from the GRÖHN-collection, and 2♀♀ from the KERNEGGER-collection. Never before so many specimens of one fossil species of acalyptates could be analysed. It is not easy to decide if only one or several species or subspecies are present among this series though one of us is familiar with the variability of extant chloropid species including *Tricimba*-species. HENNIG (1965) in his description of the badly preserved holotype added good figures, which only omitted (1) the continuation of the spinu-

lae along the hind edge of the eye down to the height of the lower point of the figured 3<sup>rd</sup> antennal article, (2) hairs on the front side of the 1<sup>st</sup> coxa, (3) hairs on the lower side of the stem of the proboscis, (4) a well observable pubescence around the 3<sup>rd</sup> antennal article which is equal in its length to the diameter of the basal diameter of the arista and (5) three moderately impressed longitudinal grooves along the central mesonotum (Fig. 19 in the present article), a peculiar character among amber acalyptates, shared only with *Protoscinella* sp.n. and *Tricimba* sp.n. (as well the extant further genera *Aprometopis* BECKER, *Pseudotricimba* ISMAY and *Tricimbomyia* CHERIAN). These grooves are accompanied or "filled" by a "criss-cross" arrangement of acrostichal micro-setulae, just as in the genus *Tricimba*, extant, or fossil, inclusive checked undescribed species from Dominican amber. The newly detected inclusions revealed two highly interesting features important in systematics of Acalyptatae: All world members of the family Chloropidae can be identified to the family level by a sharp dorso-ventrally running ridge at the fore-edge of the propleuron (anterodorsally of the first coxa), at first used in a family key by MALLOCH (1948). As this line is situated very near to the back of head its detection in side-view is not easy. The second peculiar family-specific structure is a slight flexure or kink in the basal part of the 6<sup>th</sup> longitudinal wing vein reaching the costa, namely  $m_{3+4}$  (=  $M_{3+4}$  = CuA), which marks the very point where two lost veins belonging to the ground-pattern of flies, the "basal-medial cubital cross-vein" tb (= bM-Cu) and the "anal cross-vein" (= CuA<sub>2</sub>) coalesced with the longitudinal vein  $m_{3+4}$  (abbreviations outside round brackets used here in accordance with the discussed monograph of HENNIG [1965], those inside parenthesis after MERZ & HAENNI [2000]).

The following selected 16 characters (in our protocols noted for each specimen) are subject of interesting transformations, which are judged here after a dash as plesiomorphic (ancient), apomorphic (progressive) or as a questionable condition.

(1) In the description of the holotype short but distinct ocellar bristles (oc) are figured, divergent and bent backwards (an important direction in world chloropid taxonomy, partly used in keys for the genus level). The ocellar tubercle, situated within a larger bare ocellar triangle, not figured by HENNIG, is covered by tiny irregular setulae, too weakly figured in HENNIG's description. These setulae are always present. The ocellars, normally stronger than the setulae, never are longer than in HENNIG's figure, often they are shorter, partly they are parallel and not divergent, partly they are upright and not pointing backwards, partly they are not differentiated in thickness or length from the surrounding setulae,

in such a case to be judged as "absent". — Backwards or absent: apomorphic.

(2) The distinct pubescence of the always dark 3<sup>rd</sup> antennal segment (not figured by HENNIG, see 2<sup>nd</sup> paragraph above) ventrally of the basis of the arista is bent forwards for a short distance, than abruptly it is continued without space but bent upwards. The transformation series includes both, short and long pubescence, the latter being the exception in extant Chloropidae. In living chloropid species such a difference in the length of the pubescence could be used for species definitions, we know such a case in an otherwise inseparable European new *Conioscinella*-species reared by M.v.T. from cones of Norway spruce. — Long: apomorphic, compare figures of *Tricimba* spp. in ISMAY (1993), especially that for *T. antennata* ISMAY.

(3) HENNIG figured 20 mico-setulae on the upper side of the wing vein "radius 1" ( $r_1$ ), an important character for taxonomy of Acalyptratae and singular in Chloropidae, occurring only in the fossil genus *Protoscinella*. (Rows of hairs in another combination on the lower and upper side of the veins  $r_{2+3}$  and  $r_{4+5}$ , respectively, are present in *Cestoplectus intuens* LAMB from Sri Lanka (LAMB 1918: 391-2). HENNIG's figure cannot be confirmed for the holotype because the specimen now is embedded in Canada balsam, the setulae are not countable any more. In our series no specimen was found with so many setulae. As these setulae are pointing distally in the very direction of the vein fundamentally they are very difficult to detect against their dark background, counting needs observation in extreme profile at a magnification of at least eightyfold. Intensive cold-light illumination must be used from all directions. The basal socket of each setula can be seen rarely as a light or a dark point against the surrounding resin. The number of setulae partly is different in the right and left wing. Variation includes 1 till 12 setulae, also the length of the setulae varies. The following numbers were counted checking 57 visible wings (number of setulae/ number of wings) 1/1, 2/4, 3/4, 4/2, 5/7, 6/8, 7/6, 8/9, 9/6, 10/6, 11/2, 12/2. The detection of one single similar setula on the distal end of both  $r_1$ -veins of an undescribed Asteiidae (see couplet 25a of the key), which is bent sideways and distally, is highly interesting. — Few setulae: apomorphic.

(4) A peculiar group of four short upright bristles in the supra-alar position is figured by HENNIG (l.c.), two longer and two shorter ones. In profile they can be distinguished from the more close-fitting mesonotal bristles, which follow centrally and backwards. From none extant chloropid-genus such a group is known, species belonging to the plesiomorphic Siphonellopsinae possess only one single sa-bristle, in other chloropids this

bristle has been reported to be absent. But LAMB (1918: 391-2) describes just this bristle from *Cestoplectus intuens* LAMB, 1918 (Botanobiini), and CHERIAN (1989) from the strange looking *Tricimbomyia muzhiyarensis* CHERIAN, 1989 (Tricimbini), both belonging to the Oscinellinae subfamily in modern taxonomy. BECKER (1911: 39) described a supraalar bristle and two notopleurals in his new genus *Ochtherisoma* from Australia, later sunk as a younger synonym of *Aragara* WALKER, 1860. Emilia NARTSHUK was so kind and checked this genus from the St. Petersburg collection: "I cannot see a supraalar, only 1+2 notopleural setae". The fewest world genera have been investigated in this context, and discovery of an ia in other oscinelline genera can be awaited. In our series in principle such a group of bristles is present, sometimes including more, sometimes fewer setae, mostly one or two or three longer and 0-4 smaller ones. Synchronously embedded specimens (see Table 1) possess different sets of ia, which verifies the variation at the same time segment. But one single bristle, the ground pattern in acalyprates, rarely occurs in *Protoscinella*. Such a condition is found in our *Tricimba* sp.n. with its extremely similar habitus. — More than one bristle: apomorphic in the light of size-reduction of bristles in the chloropid family.

(5) The scutellum of the holotype, flat above as in all further specimens, bears three lateral bristles (la) near the apical pair of scutellars. The whole scutellum is rugose (coarse, tiny pits each equipped with a micro-setula). Such an appearance makes it difficult to decide if in a lateral position thicker and prolongate setae are present. As in extant and our fossil *Tricimba*-species the lateral side of the scutellum tends to become perpendicular and it is as well equipped with the rugosity. Our series shows all conditions, apical scutellars alone, thin and short, or slightly thickened and elongate lateral ones, surely not homologous with the true lateral bristles in dorsolateral or lateral position of the basal half of the scutellum of other acalyprates. — Some few cumulative extended lateral bristles near the apicals: apomorphic.

(6) In the chapter "Diversity and Apomorphy" the peculiar curvature of vein  $m_{3+4}$  was mentioned. HENNIG indicated this kink in his fig. 316 by a tiny notch. In some exceptional extant chloropids among more than 2,000 valid species this curvature, expression of the phylogenetic background, disappeared. MALLOCH (1940: 261) mentioned the genera *Siphunculina* RONDANI, 1856, *Tricimba* LIOY, 1864 (under its synonym *Euhippelates* MALLOCH, 1925), and *Platyina* MALLOCH, 1927. Among others it can be observed in the abundant European *Elachiptera cornuta* (FALLÉN, 1820). Our series shows that the process of downsizing of the anal cell (=

$\text{CuA}_2$ ) was still in progress during the Eocene. Different from all extant chloropids in several inclusions a small and narrow nearly closed anal cell (= cup, posterior cubital cell of modern manuals) is developed, in others the apical closing cross-vein is only noticeable as a weak fold, a contradiction to the definition of modern Chloropidae in all handbooks. Even a faint remnant of the tb-crossvein (= bM-Cu, separating dm and bm cells after modern terminology) is visible in several specimens. It is not joining the  $m_{1+2}$  (= M) in a more or less right angle but in front of it it curves proximad (direction to the wing base) "demonstrating" its ancestry from a longitudinal vein. A dispute about the phylogenetic background of the ground pattern "flexure of the  $m_{3+4}$  vein" is solved now on the basis of our fossil species. With the distal end of this vein, equal with the notch in HENNIG's fig. 319, the rudiment of the anal cross-vein is joined, too. Last not least no remnants at all are detectable of two veins, the anal vein,  $a_1$  (=  $A_1 + \text{CuA}_2$ ) and the axillaris,  $a_2$  (=  $A_2$ , posterior branch of the anal vein). It is of high interest that already in Eocene all these rudiments were finished or highly advanced. — A fragmentary not fully closed anal cell and a tb (= bm-cu) both faintly present: plesiomorphic.

(7) Chloropidae do not possess a complete subcosta, in several extant genera worldwide this vein is hardly detectable as a short basal fold even missing its faded distal part. In the series of *P. electrica* partly an obvious developed fold can be observed ending farer proximal of  $r_1$  than indicated in HENNIG's fig. 319. A subcostal break is narrow, not indented and not accompanied by special setulae on the costa, sometimes very difficult to detect. Some few extant chloropids like species in the genus *Pemphigonotus* LAMB, 1917 miss this break, which is possibly a plesiomorphy. — A throughout its length visible weak sc and a tiny costal break: both plesiomorphic.

(8) The mesonotum (= scutum) of some few extant Oscinellinae may possess 2, 3 or 5 moderate or deep grooves, partly accompanied by rugosity and criss-cross arrangement of accompanying microchaetae in all transformation conditions. Weak expression for example is present in several species of the genera *Coenoscinella* DUDA, 1929, *Aphanotrigonum* NARTSHUK, 1964 and *Oscinimorpha* LIOY, 1864, strong expression in *Tricimba* LIOY, 1864, *Aprometopis* BECKER, 1910 and *Tricimimya* CHERIAN, 1989. The last genus can be ordered in the nearest relation to *Tricimba* and *Protoscincella*, the presence of the sa-bristle in all three has its common phylogenetic background. If the sa- and  $r_1$ -bristles are overlooked in these small flies, they would be identified as typical members of the genus *Tricimba*. The different specimens of our series exhibit slightly different

depths of the grooves. — Deep grooves: apomorphic.

(9) Prolonged probosci evolved in several genera of Chloropidae, as well in Oscinellinae as in Chloropinae. During this process mostly the number of pseudotracheae of the labellum (distal soft symmetric part of the proboscis) was remarkably reduced. Like in the acalyptrate fly family Milichiidae, the sister family of Chloropidae, several extant kleptoparasitic chloropid species can be observed participating in the meal of spiders, dipping their mouth parts in the pre-digested prey. One interesting example from Greece reported by HARKNESS & ISMAY (1976) may be cited here. Such a behaviour could be suspected also for *P. electrica* in the past because of its long proboscis, which in optimal preserved specimens exhibit a bifurcated acute tip and only 2 or 3 pseudotracheae each side, quite a low number compared with "normal" extant chloropids. No transformation series is detectable; the length of the proboscis remained stable through millions of years! In contrast to that we observe a high intraspecific variability within the abundant European *Oscinimorpha minutissima* (STROBL, 1900) and three European *Trachysiphonella*-species concerning the length of their extended probosci (*T. pori* HARKNESS & ISMAY, 1976 has an exceptional long proboscis as verified by M.v.T. in new Greek material from Lake Kerkinia). — Long proboscis: apomorphic.

(10) In extant chloropids long probosci are mostly accompanied by extended palpi, an example is again the species *O. minutissima* mentioned above and in addition *Siphonella oscinina* (FALLÉN, 1820), developing in spider cocoons. The palpi of *P. electrica* underlie certain variability from normal and robust till slender and long, from yellowish till dark. — Long thin palpi: apomorphic.

(11) Prescutellar bristles (prsc) in Oscinellinae, to which *Protoscincella* belongs, are often difficult to detect as they are standing very near to the suture between mesonotum and scutellum and often are scarcely longer than the acrostichals adjoining in front. Distinction may be possible by their slightly more robust appearance. In amber specimens their counting turns out to be difficult as well from dorsal as from oblique lateral. The holotype clearly has well developed prsc but our series shows all conditions: prsc absent, each side 1 slightly elongate or short, 2 short, 3 short ones in one transverse row, both sides together 10 bristles including the inner postalars (ipa) and dorsocentrals (dc). The outer postalars (epa) are distant and do not appear as members of this "row" — One prsc plesiomorphic; 0, 2 and 3 prsc apomorphic.

(12) In *P. electrica* the ipa insert exceptionally near to the scutellum compared with extant Oscinellinae.

**Table 1:** Collocation of aggregated acalyprates in one piece of amber. Each comma separates one stone.

Family	Species	♂♂: ♀♀
Camillidae	<i>Protocamilla</i> sp.	2:3, 2:0, 1:2,
Campichoetidae	<i>Pareuthychaeta electrica</i>	2:6, 1:1
Campichoetidae	<i>Pareuthychaeta minuta</i>	1:2, 2:0
Campichoetidae	<i>Pareuthychaeta</i> sp.	2:2
Chloropidae	<i>Protoscinella electrica</i>	2:1 + 1 Acroceridae, 2:0, 2:0, 2:0, 2:0, 0:2
Chyromyidae	<i>Gephyromyiella electrica</i>	1:2
Cypselosomatidae	<i>Cypselosomatites succini</i>	1:1 in copula
familia inc.sed.	gen.sp.	6
Heleomyzidae	<i>Protoorbellia hoffeinsorum</i>	2:0
Heleomyzidae	<i>Suillia major</i>	0:1 + 0:1 Camillidae + 1:0 inc. sed.
Heleomyzidae ?	gen.sp.	0:4
Megamerinidae	<i>Palaeotanypeza spinosa</i>	0:1 + 0:1 <i>Palaeotimia lhoesti</i> ,
Dryomyzidae		
Micropezidae	<i>Electrobata tertaria</i>	0:3
Milichiidae	gen.sp.	1:3, 4:0
Proneottiophilidae	<i>Proneottiophilum extinctum</i>	0:4 + 2 + 1:0 + 1:0 Heleomyzidae (coupl. 89b)
Psilidae	<i>Electrochyliza succini</i>	2:0
Sciomyzidae	gen.sp.	2:1

**Table 2:** Species of acalyprates identified from both deposits, Baltic and Bitterfeld.

Anthomyzidae	<i>Protanthomyza collarti</i>
Camillidae	<i>Protocamilla succini</i>
Campichoetidae	<i>Pareuthychaeta electrica</i>
Chloropidae	<i>Protoscinella electrica</i>
Cryptochaetidae	<i>Phanerochaetum tuxeni</i>
Diopsidae	<i>Prosphyracephala succini</i>
Drosophilidae	<i>Electrophortica succini</i>
Heleomyzidae	<i>Electroleria alacris</i>
Heleomyzidae	<i>Suillia major</i>
Heleomyzidae	" <i>Heteromyza</i> " <i>dubia</i>
Milichiidae	<i>Phylloomyza jaegeri</i>
Pallopteridae	<i>Pallopterites electrica</i>
Proneottiophilidae	<i>Proneottiophilum extinctum</i>
Pseudopomyzidae	<i>Eopseudopomyza kuehnei</i>
Psilidae	<i>Electrochyliza succini</i>

Thus they may be overlooked or allocated wrongly. In the figure of HENNIG they were omitted. The holotype is embedded in lateral position, became blackish and is enfolded in iridescent fissures, the prsc are masked. In the series they rarely are absent but, if present, they always insert adjacent to the edge of scutellum. — Absent: apomorphic.

(13) Fig. 314 in HENNIG's monograph (l.c.) shows a small setula between the vertical bristles vte and vti, rarely to be observed in acalyprates. In our series this setula mostly inserts in the same position, rarely outside of the vte. — Position without judgement.

(14) Eyes of *P. electrica* are mostly covered by dense long pubescence confirmed also for the holotype. Some specimens only possess dense short pubescence, in some others these fine microchaetae cannot be detected. Both conditions occur in extant species of the sister genus *Tricimba*. — Judgement uncertain.

(15) Cerci (posterior appendages in the male epandrium) were not described by HENNIG as the sex of the holotype could not be ascertained by him. One of us (M.v.T.) identified it as a female. All our males, 50% of all specimens, possess large-scaled rounded cerci with long hairs around their edge. Their outline, well to be seen in lateral view, shows slight variation towards a more acute lower posterior end in some few specimens. — Not evenly rounded: apomorphic.

(16) The length of body and wing of each specimen (24♂♂, 21♀♀) was measured. With one exception the ratings show a Gaussian distribution: Body (without ovipositor and antennae): 1.52-2.52 mm, on average 2.06 mm; wing 1.35-2.03 mm, on average 1.70 mm. One well preserved female with identical morphology is placed far outside these ranges: body 3.11 mm, wing 2.40 mm. — The normality in 44 specimens supports that only one species is involved. Extreme sizes, short or long, are not connected with plesiomorphic or apomorphic conditions of other characters.

Palaeontologists working with marine or freshwater organisms and their rich material of transformation series from much longer lasting geological periods will not understand our enthusiasm. But terrestrial animals normally underlie quicker changes of climate conditions and other unbuffered catastrophic events. Their fossil record is always extremely poor. For a dipterist confronted with the tremendous difficulties in species separation of our present fauna *P. electrica* is an impressive example for the slow evolutionary process of altering minute characters all appearing to be independent from one another. Finally the discussed transformation series ended in at least one further *Protoscinella*-species (with much smaller 3<sup>rd</sup> antennal segment, different cerci and other reductions) and the first detected fossil *Tricimba*-species (with all characters of extant *Tricimba*-species, except a present sa-bristle of the fossil) both included in our key. Hundreds of extant *Tricimba*-species are distributed worldwide, which in a large extend are still undescribed. The never-ending discussion about whether genera of the Tertiary age are surviving to date can be answered without hesitation: Yes! *Protoscinella* and the mentioned millipede and spider genera from Baltic amber are best examples.

## Antiquity and palaeoethology of schizophoran flies

GRIMALDI et al. (1989: 20-22) presented a photograph of a Cretaceous fly from New Jersey resin deposits which they identified as a possible member of the family Milichiidae. Their decision is accepted by us, as the typical habitus with its curved dorsal surface, the prolonged thick palpi and the elongate proboscis with elbowed labellum are typical for most extant Milichiidae, too.

Recently GRIMALDI commented the 20 years old record (pers. comm.): "Unfortunately, the age of the milichiid in New Jersey amber (in the same piece as the stingless bee) is uncertain, and almost certainly no older than latest Cretaceous. The strata that produced the piece (from an old collection) have never been identified."

Older records of acalyprates or the whole group of Schizophora (= Acalyptratae + Calyptratae) from the Mesozoic are not mentioned in the latest attractive book overview on fossil insects (GRIMALDI & ENGEL 2005). Only MCALPINE (1970) described remains of a much older fly, 11 aggregated puparia of *Cretamorpha fowleri*, Calliphoridae, a family of the Calyptratae, of Late Cretaceous age, 70 million years ago. GRIMALDI & ENGEL doubt the correct family identification but accept that those puparia belong to the Cyclorrhapha. The oldest record of Schizophora flies are mentioned in a list of "Organisms found in Late Cretaceous (Turonian) amber at the Linden Sand Pit, Sayreville, New Jersey, JOHNSON/DILLON Collection", "90-94 million years old" by GELHAUS & JOHNSON (1996: 62, 55): five Acalyptratae without family determination and one Chloropidae. Let's stay with the Tertiary fauna: nearly fifty million years passed without any new evolutionary process based on progressive developments concerning the ground pattern of bristle arrangement or other morphological details. All reduction lines or luxurian genitalia peculiarities were already present during the amber times. The external similarity of Tertiary Acalyptratae with the extant world fauna leads to the speculation that the past fauna was as diverse as nowadays. More than 1,100 checked new fossil acalyprates let at least 161 undescribed species appear and no end of this multiplication is in sight! A reason that so much more specimens of Phoridae, Dolichopodidae, Empididae and Hybotidae were embedded in resin – compared with the acalyprates – could be their behavior and ecology: a much higher abundance, a more powerful flight activity or their higher preference for forests. We have to consider that later periods were dominated by grazing ruminants and horses, which promoted the speciation of herbs and grasses (Poaceae) and the decline of forests in favour of prairies and other open landscapes. The behaviour of visiting sunny spots and other shiny struc-

tures within the forest shade promotes sexual display and rising of body temperature. Together with all the other ecological details such insect activities are common observations as well in forests of lower geographical latitudes as in tropical rainforests. Single amber pieces with hundreds of preserved Dolichopodidae belonging to one species only tell us this story of assembling behaviour, which never has been documented for amber Acalyptratae. Among our 1,141 stones with acalyprate inclusions all 32 stones with aggregated acalyprates of one or some few species are presented in this connection (Table 1). The documented numbers are too low to detect a statistically confirmed imbalanced sexual-index.

## The German Bitterfeld Amber – evidence for its contemporaneous genesis with Baltic Amber

Since many years in Germany an ongoing dispute "Bitterfeld amber versus Baltic amber" divides stalwarts and disputants. The discussed hypothesis of the presumed autonomy of Bitterfeld amber being of a younger age initiated a research for conspecific inclusions. WEITSCHAT (2008) listed 163 identical species, which were identified from both deposits, the Baltic and the Bitterfeld one. Details are translated above in the chapter on the duration of amber times. To date at least 15 conspecific species of acalyprate Diptera, all described by MEUNIER and HENNIG, occur in Baltic as well as in Bitterfeld amber (Table 2), that is a ratio of 27% out of the 56 described taxa. We await more species to be selected from both deposits when the large material from private collections becomes checked. On the basis of these identical findings the hypothesis of a separate genesis cannot be supported. We confirm a contemporaneous Baltic and Bitterfeld amber fauna by a listing of all confirmed species from the Baltic region as well as from Bitterfeld (Table 2).

## Important morphological characters to identify "Acalyptratae"

Recognizing Acalyptratae is not easy, which is one of the reasons why this group of flies has been neglected in amber research. Our support with inclusions was promoted after repeated personal instructions to friendly amber dealers who became really specialists in detecting and separating these rare "small bristly flies" (GELHAUS & JOHNSON 1996). Beginners in dipterology can select Acalyptratae "cum grano salis" after twelve features (unfortunately all but one, no. 7, with exceptions):

**a) Helpful for the detection of an acalyprate but without systematic value:** 1) no metallic sheen; 2) body rarely completely polished; 3) legs bare or with rel-

atively few strong bristles; 4) these bristles rarely braced in different divergent directions; 5) tibiae in addition to the all around micro-setulae mostly bare or only with some few very short bristles at their distal end or in preapical or posterolateral position, if spines in apical position mostly only in one leg; 6) head more or less round and not strongly excavated at rear, rarely shortened or elongate, gena (= cheek) below eye present; 7) eyes not very narrow approached or in touch in front of the ocelli; 8) rarely huge male genitalia present, which are well and movable separated from the last tergite, with long appendages and stiff bristles, and pointing downwards; 9) arista mostly inserting on the dorsal basis of the 3<sup>rd</sup> antennal segment, not at its tip; 10) tip of 3<sup>rd</sup> antennal segment not extended in a very acute tip carrying the arista.

**b) Taxonomical important characters:** 11) a lunule above the base of the antennae bordered above by a half-moon shaped or lesser arcuate line or interruption against the frons (the ptilinal fissure); 12) The mesonotum (= scutum) is divided in an anterior and posterior part, both separated by an incision, the transverse "suture", which does not run across the whole mesonotum but ends each side lateral of the row (each side one) of dorsocentral bristles (or their prolongation if such bristles are present only far behind). A complete suture (without central interruption) belongs to the rarest amber inclusions, the Calyptratae (one species was described by MICHELSSEN 2000). Therefore all the distinguishing details against this group of modern flies (to which the house fly belongs) are unneeded here. An extended and acute ending anal cell (= CuP) is absolutely rare in acalyptbrates, but a short or tiny tip at its distal end seldom occurs and points out a plesiomorphic evolutionary condition.

Many controversial opinions about the systematic position, monophyly or paraphyly, of the so called "Acalyptratae MACQUART, 1835" (wrong spellings: Acalyptera, Acalypterae, Acalyprata) within the Cyclorrhapha, Muscomorpha, Schizophora, were published during the last twenty years following the publication of a detailed investigation by GRIFFITHS (1972); some of these were discussed by VON TSCHIRNHAUS (2008). The taxon with its morphological background serves still as a good hypothesis for taxonomical work and a practical basis for ecological fieldwork and sorting of alcohol preserved trap material.

The following checklist (Table 3) eases the determination of fossil and extant acalyptbrates and can be used for protocols about each single investigated specimen. It contains nearly all the important characters helpful for the discrimination of species. Moreover, it prevents the loss of sight on a special detail. The sequence follows

practical experience with the manipulation of inclusions during the stereoscopic study, most suitable progressing from front to rear, and from bristle details to the whole habitus aspects. It includes not only all characters used by HENNIG in his latest key (1969) but provides space also for further criteria partly neglected hitherto. The abbreviations are used in accordance with HENNIG, some few have been increasingly shortened (ap, la, st), one created for the first time (dpr); in Table 4 the new ones are printed in bold. The right column of the sheet normally is empty, here we use it only to explain which questions in addition to the foregoing column should be answered or at least checked. Question marks after all thought-provoking impulses are omitted. The identical numbering sequence is used again in the additional identification key for peculiar characters or their combinations. In the prefixed key for 97 peculiar characters partly more than one item belongs to one number of Table 3. Thus, its items all are carrying sub-numbers in the exponent position, also in order to distinguish them fundamentally from the couplets of the main key. In the identification couplets the very sequence is also kept after the semicolon, which is followed by the listing of documented details not used for a check at the first glance; characters for a quick view are listed in front of the semicolon.

## How to use the key?

Our translation of the original German key of HENNIG (1969) with his amendments (1971) is as close as possible. In order to shorten the key most abbreviations of complete scientific terms have been used in just the same manner as HENNIG used them. Table 4 lists the well known and more than hundred years ago introduced European abbreviations and terms which were also used in the keys of HENDEL (well figured; 1928), the series "Die Fliegen der paläarktischen Region" (LINDNER 1949), the key for all world families of Diptera (HENNIG 1973) and the key for the Afrotropical Region (BARRACLOUGH 1995). Together with the complete English terms they are opposed to the "new" names widely used since the publication of the "Manual of Nearctic Diptera" (MCALPINE et al. 1981b) and taken over by MERZ & HAENNI (2000) in chapter 1,1 for the whole manual edited by PAPP & DARVAS. Also OOSTERBROEK (2006) and BUCK et al. (2008) in their fantastic family keys for Diptera followed this new terminology. Thus, the multitude of 426 morphological figures in HENNIG's series of amber publications on acalyptbrates (1965, 1969, 1967, 1971, 1972), his species descriptions and elaborate phylogenetic discussions can be used all without difficulties in termini transfers. All alternative question couplets, translated as literal as possible, are only those of HENNIG (l.c.) but with corrections of obvious mistakes and some

**Table 3:** Protocol sheet with questions for the determination of single inclusions of "Acalyptratae" in Baltic amber. Line numbering is used in the first part of the key. More information in the text.

Key (Hennig 1969) couplet:		Collection, code:	Inclus.
Family:		Species:	
1	body / wing length in mm	all measures without antennae, females with and without ovipositor	
2	vi + peristomal b.; clypeus	1 (or rarely 2) vi; number; prominent; fills whole mouth width, shiny	
3	ors (ors+ori); orbital setulae	number, position, direction, weakness; (along eye) pro- or reclinate	
4	if 0 or present, direction	some longer, ordered along mid-line, 2 proclinate crossing lunule	
5	oc (pro- / reclinate, upright)	position, weak, strong, bent in-, back-, or outwards	
6	pvt (convergent, divergent)	reclinate, upright, proclinate, size	
7	occ bristles; occiput cove	center of back of head with b.; concave, flat, convex, vertex saddle-like	
8	vte + vti	present, absent, if one shorter which	
9	hind edge of eye	lower side retreating, above with 1 or 2 b.-rows, bent up- or downwards	
10	h (0, 1, or 2)	size	
11	n + n (0+1,1+1,1+2, or more)	anterior + posterior, position of hind one (note only if higher)	
12	prs (0 or 1)	size	
13	pteropleural bristles	0, 1 , or more (below wing base)	
14	pp (0, 1, or 2, size)	on anterior or posterior part of propleura (separated by a vertical seam)	
15	mesopleural hairs	absent, present, allocation; pubescence (= pollen, = dust)	
16	m	number, position, weakness	
17	st	number, position, weakness; sternopleura haired or bare	
18	dc (count from behind)	postsutural + presutural, size, if postsutural only: position	
19	all prsc between dc-rows	add both sides, either 0, 2 or rarely 4 or 6, size	
20	ia (0 or 1)	between sa and dc-row, or in front of ipa	
21	epa + ipa	both present, one missing, which; size, position of ipa	
22	sa (0 or 1)	in rare cases very small and more than 1	
23	acr-rows between dc-lines	don't include the acr-row in the very dc-line	
24	la (0, 1 or more)	additional bristles on the disc of scutellum, size comp. with ap, position	
25	ap (size, curvature, distance)	inserting on warts or projections, upright, divergent, comp. size with la	
26	scutellum bare	surface convex or flat, pubescent or shiny; shape of scutellum	
27	scutellum haired	surface rough (rugose) with hairs in pits or normal setulae	
28	f1 bristle/spine arrangement	dorsal, posterodorsal, posteroventral, ventral, anteroventral, anterodorsal	
29	f2 ditto	ditto, special attention to 1 anteroventral /-dorsal (Sciomyzidae-type)	
30	f3 ditto	ditto, special attention to 1 or 2 ventral rows of spines	
31	t1 t2 t3:1 dorsal preapical b.	end-bristles or spurs, cleaning comb at end of t1 or / and end t3	
32	femora peculiarly thickened	(or peculiarly slender), which one, f straight or curved	
33	costal-spinules; sc-cell	absent, long, short, standing apart; sclerotized and dark, short or long	
34	r1-setulae; length of r-veins	present, above, below; r2+3 shortened, curvature of each r-vein	
35	costa ends at m1+2 or r4+5	wing tip at r5 or m1, between both, or behind r4+5, r5 and m1 convergent	
36	sc complete	normal or bent strongly (90°) forwards to costa	
37	sc is a fold distally	add a ? if observation not quite sure	
38	sc ends near to r1	a swelling of end of r1 may touch the sc then continuing separately	
39	sc ends far from r1	either complete or as a fold or absent; between sc and r1: subcostal cell	
40	subcostal-break, hum.-break	bristles at end; further costa-break distally of humeral crossvein	
41	tp : m3+4-end section	longer or shorter, tp oblique on m3+4, basal angle obtuse or acute	
42	end of anal cell	(modern term: CuP) acute angle or rounded end, analis and a2 present	
43	ta-position on discal cell	posterior cross-v. basal, apical, in mid of discal (modern: dm) cell	
44	metathoracic spiracle bristle	absent or present, note also fine hairs (rare in Sciomyzidae)	
45	scapular bristles	inserting on front of thorax (bent towards head) absent or present (1 or 2)	
46	face concave, flat, convex	a keel present between 1st antennal segments, ending at level of ...	
47	gena : eye height (or t1-0)	width of gena + parafascialium (below eye) compared with eye height	
48	shape of palpus; proboscis	short, long, thick, widened distally, bristles, colour; narrow & elongated	
49	3rd antennal article, arista	shape: round, elong., tapered, a ball, pubesc.; position, pubesc. or rays	
50	2nd antennal article	cap-like, an outside extension, dorsal bristle, dorsolateral cleft, elongate	
51	genitalia, cerci	appendices on epandrium, sternites, pleura; oviscape, shape of cerci	
52	5 or 6 tergites, pseudotergites, body colour, shape and width of head, eye and body pubescence, etc.:		
53			
54			
55	preservation status of fly and stone, measures of the stone, date of protocol		

stellate hairs present / absent

few necessary enlargements. Corrections and enlargements are written in a different, slightly larger font.

Some newly detected peculiar Acalypratae and some others with outstanding features hidden in HENNIG's key provoked us to prefix a special (but possibly incomplete) overview of rare characters, combinations and morphological details of phylogenetic interest, partly completely unknown to occur in Acalypratae (e.g. items metatarsus and calypter). Reading HENNIG's detailed amber publications thoroughly some more cross-reference ciphers may be added. The buildup also points out which bristles of the groundpattern – either in the amber period or in today – are reduced very seldom, e.g. the ocellar or supra-alar bristles. It may also be helpful for the reader not interested in identifying an inclusion. The sequence of the 97 items 2<sup>1</sup> to 52<sup>6</sup> is ordered and numbered according to the protocol-sheet, Table 3. In case of bad preservation of an inclusion the buildup enables a quick identification without running through the whole key pointing out where to search the appropriate couplets or their amendments.

All newly detected and analysed species of Acalypratae are not included in alternative question couplets, which would have been a giant work considering, that much more fossil acalybrates await discovery. They rather follow a HENNIG-couplet with a numbering by lower case letters (the letters j and o were omitted). Each lower case, which represents an undescribed species, is followed by "sp.n." with a consecutive numbering. Rarely cross-references are added leading to other key-couplets. The amendments numbered with lower cases partly contradict HENNIG's main couplet, which combines several features, which do not apply all to the detected following new species. HENNIG's original question was only rarely amended (and underlined) in order to apply also for the following new species. Amendments do not follow a special system; they express the chronological sequence of detection of the new species by one of us (M.v.T.).

There is a reason to note measurements with two digits after the decimal point:

Subsequent workers can recognize the very specimens of the VON TSCHIRNHAUS-collection easier; measurements mean bodies and wings in their natural horizontal position under a grinded and polished flat amber surface, first without antennae and without expanded soft ovipositors, last including the whole root of wing. Accuracy of measures were ±0.025 mm for all lengths until 2.5 mm, ±0.05 mm for all from 2.51 until 5 mm, and ±0.1 mm for all larger than 5 mm.

The shortened list of characters for the undescribed species usually do not repeat characters already passed

through and answered in the foregoing couplets. The most peculiar characters are standing in front concluded by a semicolon. All other features, separated by commas, are following in the succession as shown in the file sheet (Table 3) and the listing below, the order of which eases microscopic manipulation. The ciphers (couplet plus a lower case) represent the collection number in the VON TSCHIRNHAUS-collection. There, in addition, each specimen is numbered continuously, always beginning with number 1. The file-sheet for each specimen comprises more detailed morphological descriptions and notes, including a list of all other accompanying syn-inclusions. Stellate plant hairs are always mentioned there, as they are a confident proof for Baltic amber.

The following pattern of bristles and characters judged as "normal" is not always mentioned in the key amendments though they all have been recorded. Exceptions are cases of the distinction of two similar species running to the same main couplet. The sequence of 44 characters follows Table 3:

- A normal clypeus (praelabrum) not filling the whole width of the mouth opening and not protruding convex forwards over the mouth margin • one or two rows of small or strong peristomal bristles • all ors only bent backwards (reclinate) • the surface of frons, bare or covered with small interfrontal setulae (if), as far as these are not twin and extended • proclinate-divergent oc • vte and vti present • 1 h • 1+1 n (anterior and posterior) • 1 prs • separation of the number and position of anterior and posterior pp bristles (inserting on proepisternum and proepimeron) • mesopleural and sternopleural hairs present or absent • 0 ia • 1 epa + 1 ipa • 1 sa • more than 2 rows of acr between dc-rows • 1 la +1 ap • ap longer than la • bare or haired surface of scutellum • detailed bristle pattern of all femora • tibiae bristling including apical tibial spurs and • tarsi • cleaning combs and • metatarsal brushes • femora not peculiarly thickened • costa without spinules in addition to the normal setulae • subcosta cell not sclerotized or darkened • costa running to m<sub>1+2</sub> • position of wing tip in relation to the endings of veins r<sub>4+5</sub> and r<sub>1+2</sub> • r<sub>1</sub> without setulae on upper side of wing • r<sub>4+5</sub> and r<sub>1+2</sub> parallel or slightly divergent in distal part • sc complete till end • end of sc far from r<sub>1</sub> • costa without breaks • both crossveins, ta and tp (= R-M and DM-Cu) present • anal cell not ending in an acute tip or small point • presence and length of anal vein (= A<sub>1</sub>+CuA<sub>2</sub>) and axillaris (A<sub>2</sub>, posterior branch of anal vein [the importance of this vein in acalyprate taxonomy, fossil and extant, is underestimated]) • no bristle(s) near posterior spiracle • absent scapular or "prescapular" (WOZNICA 2007) bristles • face flat without keel (neither concave nor convex) • palpi and proboscis not peculiarly thick-

**Table 4:** Terminology and explanation of chaetotaxy as used in HENNIG's amended key, with the synonyms in the "Manual of Palaearctic Diptera" (MERZ & HAENNI 2000) in squared brackets.

Abbreviation	Explanation	Manual Pal. Diptera Synonyms
acr	acrostichal setae (0 to 16 rows between dc)	
ap sc = ap	apical scutellar bristle (one at tip of scutellum, = 1 pair)	
dc	dorsocentral bristle (3+1 means: 3 behind and 1 before suture; count from behind !)	
— dpr	one dorsal preapical tibial bristle (can occur on all tibiae), abbr. not used by HENNIG	
epa	outer postalar bristle (at hind corner of thorax behind wing base)	
f1, f2, f3	femur of 1st, 2nd, and 3rd leg (the 3rd article of a leg, rarely swollen)	
h	humeral bristle (1, rarely 2 on the humeral callus)	[= postpronotal seta]
ia	intraalar bristle (1, between sa and ipa, often difficult to detect in amber flies)	
if	interfrontal setulae, mostly irregular, rarely 1 - 2 proclinate pairs are bristles	
ipa	inner postalar bristle (1, between epa and base of scutellum)	
la sc = la	lateral scutellar bristles (incl. 1 on the lateral surface, which is the exception)	
m	mesopleural bristles	[= anepisternal]
m1+2, m3+4	two media veins (6th and 7th from wing base)	[= M1+2, CuA+CuA1]
mt1, mt3	metatarsus (basal tarsus-article out of 5) of fore and hind leg	[ basitarsus]
n	notopleural bristles (mostly 2, rarely 0, 1 or more)	
oc	ocellar bristles (1, together a pair, in front of ocellar tubercle)	
occ	occipital bristles (on central back of head, only used in Tab. 3)	
ors	fronto-orbital bristles (on the sides of frons, along eye margin)	
orsa = ors	incline anterior fronto-orbital bristle (often called ori)	
orss = ors	recline superior orbital bristle (often called ors, which we don't use in this article)	
pp	propleural bristles (above front coxa, mostly 1, rarely more, sometimes minute)	
prs	presutural bristle (1, above notopleuron and in front of suture)	
prsc	prescutellar bristles (1, together 1 pair, rarely 2 or 3, between 1st dc)	
pvt	postvertical bristles (1 pair, behind ocelli)	[= postocellar setae]
r1, r2+3, r4+5	radius, 3 veins (the 3rd to 5th from wing base), r1 mostly short	[= R1, R2+3, R4+5]
sa	supraalar bristle (1, 2 extremely rare, on mesonotum above wing base)	
sc	subcosta (complete or weak vein, the 2nd from wing base)	[= Sc]
sca	scapular bristle (1 or 2 on one side, inwards of humerus)	
stpl = st	sternopleural bristle (upper edge, setulae excluded)	[= katepisternal]
t, t1, t2, t3	tibia, t1 is tibia of the fore leg etc. (t = 4th article of a leg)	
ta	anterior crossvein (between radius4+5 and media1+2)	[= R-M]
tp	posterior crossvein (between media1+2 and media3+4)	[= DM-Cu]
vi	vibrissa(e) (1, rarely 2, at anterior corner of cheeks and lower corner of face)	
vte	outer vertical bristle (1, at upper hind corner of head)	[= lateral vertical bristle]
vti	inner vertical bristle (1, at upper hind corner of head)	[= medial vertical bristle]
anal cell	anal cell (most posterior cell of wing, small)	[= cup]
analis	anal vein, from anal cell to wing margin, often abbreviated	[A1+CuA2]
antennal segments:	(= antennal articles), 1st, 2nd, 3rd	[= scape, pedicel, flagellum]
arista	bristle like 4th to 6th antennal segment, 1st is hidden	
axillaris	axillar vein / fold, the most posterior wing vein, often missing	
clypeus	(= prementum): movable sclerite on basal front part of proboscis	[= A2]
costa	the vein along the wing edge, ending mostly at m1+2, rarely at r4+5	
face	below 1st antennal segments till mouth margin, partly foveae for antennae	
frons	part between vertex of head and lunule above antennae	
humeral callus	the prominent shoulder at anterior edges of thorax	[= postpronotal lobe]
labela (...ae)	symmetrical soft part of proboscis for taking up food, carrying pseudotracheae	
mesonotum	the main dorsal slightly humpy part of the thorax	[= scutum]
mesopleuron	upper large plate on central side of thorax, behind spiracle	[= anepisternum]
metathoracal spiracle:	the posterior spiracle of thorax lateral in front of abdomen	[posterior spiracle]
orbital setulae	small hairs on the orbits, the side parts of the frons	
peristomal bristles:	1-2 rows of bristles along mouth margin, behind vi	[= subvibrissal setae]
proboscis	all movable mouth parts	
propleuron	narrow frontal part of thorax, visible above the coxa of fore leg	
pteropleuron	large plate below wing basis, mostly bare	[= anepimeron]
spur	a thick bristle at end of a tibia, partly accompanied by smaller spurs	
spine	an unmovable thorn on ventral sides of femora, partly raptorial	
sternopleuron	lower large central plate on side of thorax above mid leg	[= katepisternum]
suture	transverse suture of thorax, centrally interrupted	
vertex	the highest connection between both facet-eyes	



**Fig. 1-2:** Periscelididae, *Procyamops succini* HOFFEINS & RUNG, holotype, ♀, body 2.8 mm, lateral habitus and head profile, coll. HOFFEINS 1378.



**Fig. 3:** Campichoetidae, *Pareuthyshaeta minuta* HENNIG, ♂, body 2.4 mm, dorsolateral habitus; note the red-coloured eyes, remnants of vivid colour; coll. HOFFEINS 671-5.



**Fig. 4:** Campichoetidae, *Pareuthyshaeta* sp., sex ?, body incomplete, 2.2 mm, dorsolateral habitus; note phoretic mites (Gamasidae) behind 1<sup>st</sup> coxa (more invisible in photo between coxae); coll. HOFFEINS 671-1.

ened or elongate • 3<sup>rd</sup> antennal segment nearly round or slightly oval with arista inserting dorsally • 2<sup>nd</sup> antennal segment short and without the typical "Clusiidae-character", a triangular extension at outer surface lapsing over onto the 3<sup>rd</sup> article • 6<sup>th</sup> tergite and/or epandrium not articulated by a dilatable membrane against the 5<sup>th</sup> or 6<sup>th</sup> tergite and not bent ventrally • oviscapte absent.

## Amended key to Baltic amber acalyptate Diptera, based on HENNIG (1969)

(I: Hennig 1965, II: Hennig 1967, III Hennig 1969, IV: Hennig 1971; Hennig 1940, 1966, 1972).

2<sup>1</sup>-52<sup>6</sup>: Incomplete cross-references to peculiar characters, the sequence follows Table 3.

- 2<sup>1</sup> The six bristles vi, ors, oc, vte, vti and h all absent in one species ..... 61
- 2<sup>2</sup> As 21, but tiny oc are present, also absent are: pp, m, st, dc, prsc, and ia ..... 2d
- 2<sup>3</sup> Two vibrissae of equal size each side (teratological?) ..... 11e, 52, 88g
- 2<sup>4</sup> Hind corner of genae (= postgenae) with 2 very long and strong bristles pointing downwards, no further strong peristomal bristles, vibrissae absent ..... 79g
- 3<sup>1</sup> Orbital bristles (ors) absent (compare 3<sup>3</sup>) ..... 2d, 17c, 17d, 49b, 61
- 3<sup>2</sup> 2<sup>nd</sup> fronto-orbital bristle from behind proclinate and inserting far from eye margin and near to ocellar triangle ..... 4a
- 3<sup>3</sup> A long row of at least 10 (up to 17) evenly short ors becoming slightly longer behind ..... 32, 32a, 72a
- 4<sup>1</sup> Interfrontal bristles in two longitudinal rows (a single anterior pair neglected) ..... 52
- 5<sup>1</sup> Only one ocellus present ..... 43a, 45c
- 5<sup>2</sup> Ocellar bristles (oc) absent ..... 24, 32 pro parte, 61, 67, 68, 69, (76 tiny)
- 5<sup>3</sup> Ocellar bristles reclinate ..... 77a, 87d
- 6<sup>1</sup> Postverticals (pvt) bent forwards ..... at least 25a, 54a, 78d, (85a), 87b
- 6<sup>2</sup> Postverticals absent ..... 16h, 19i, 24, 41c, 49i, 54, 77a, 79b
- 6<sup>3</sup> Vertex between both vti concave, saddle-shaped ..... 5k, 16h, 24a
- 8<sup>1</sup> One or both vertical bristle(s) (vte and vti) absent ..... 2d, 17a, 19i, 32, 49b, 49i, 54a, 61, 68, 68b, 78d
- 10<sup>1</sup> Humeral bristle (h) absent ..... at least 16m, 18, 24, 24a, 25a, 42 l, 49a, 49d, 61, 63-69, 89h
- 11<sup>1</sup> Notopleurals absent ..... 1
- 11<sup>2</sup> Only 1 notopleural ..... 17c, 24, 24a, 25, 25a
- 11<sup>3</sup> More than 1+1 notopleurals (n) ..... 2d, 42f, 78d, 85b
- 12<sup>1</sup> Presutural (prs) absent ..... 16h, 19f, 19i, 25, 30, 33a, 40f, 42c, (42f), 42g, 42k, 42n, 49i, 54a, 58, 59b, 63-69b, 71, 73, 75c, 77, 77a
- 12<sup>2</sup> More than 1 prs ..... (19e), 78d
- 14<sup>1</sup> Anterior part of propleuron with very sharp vertical ridge on anterior section upwards to humeral callus (not visible if head closely applied to thorax), all world chloropids ..... 32
- 14<sup>2</sup> Three anterior pp (= proepisternal) and 3 stigmatal (= proepimeral) bristles ..... 88k
- 18<sup>1</sup> Dorsocentral bristles (dc) absent ..... 2d
- 18<sup>2</sup> Mesonotum brilliantly shining, or only pubescent between dc-lines ..... 25a, 89b
- 19<sup>1</sup> Directly in front of scutellum partly 4 or 6 tiny prsc present between 1<sup>st</sup> dc, arranged in one transverse row together with dc and ipa (variable number between 2 and 6) ..... 32, 61
- 20<sup>1</sup> Intra-alar (ia, between sa and ipa) present ..... 2b, 5a, 13, 14b, 17c, 19f, 38a, 42f, 44, 70, 78 f
- 21<sup>1</sup> Both epa and ipa together absent ..... 49i
- 21<sup>2</sup> Inner postalar (ipa) absent ..... 16h, 24, 32 pro parte, 42c, 68c, 74 a, 74b, 74d, 77a, 88c, 88d
- 22<sup>1</sup> Supra-alar bristle (sa) absent ..... 32 (part), 49i, 72b, 74a
- 22<sup>2</sup> More than 1 sa bristle present (if 2 in line the anterior may be called praearalar) ..... 17a, 19, 32, 32b, 40f, 42f, 88k
- 23<sup>1</sup> Acrostichals (acr) completely absent, mesonotum shining but sparsely or densely pubescent ..... 24, 68c, 81b
- 23<sup>2</sup> Only two rows of acr between the dc-lines present ..... 49i, 64a, 68a, 74c, 74d, (88c)
- 23<sup>3</sup> Only one row of acr between the dc-lines present ..... 25a
- 24<sup>1</sup> Lateral scutellar bristles absent ..... 1, 16, 24, 24a, 68, 68b, 68c, (69), 72b, 74c, 76, 82b
- 25<sup>1</sup> Apical scutellars (ap) much shorter than lateral (la) ..... 14
- 28<sup>1</sup> Outer tip of fore-coxa with an acute sclerotized small protuberance ..... 68c
- 31<sup>1</sup> All tibiae with an uncommonly rich equipment of long bristles ..... 11h
- 31<sup>2</sup> First and 2<sup>nd</sup> leg with broadened 1<sup>st</sup> and 2<sup>nd</sup> articles of tarsi ..... 19h
- 31<sup>3</sup> Metatarsus of first leg with an appendix or long hairs (only in males ?) ..... 5b, 5c, 51
- 31<sup>4</sup> Metatarsus of first leg thicker than tibia, all around matt, densely pubescent ..... 24a
- 31<sup>5</sup> First leg with a strong spine (thorn) in the ventral mid of its femur ..... 0a, 5b, 5g, 5i, (5l), 47, 47b, 52c, (73)
- 31<sup>6</sup> Mid leg of male with strongly broadened 2<sup>nd</sup> and 3<sup>rd</sup> tarsomere, 4<sup>th</sup> also widened ..... 19h

- 31<sup>7</sup> Metatarsus of 3<sup>rd</sup> leg shortened and thickened, thin long arista pointing sideways ..... 0b  
 31<sup>8</sup> All tarsi with claws not evenly curved but bent over in an abrupt angle ..... 43a  
 34<sup>1</sup> One setula (25a, 32 part) or a row of setulae on upper side of 1<sup>st</sup> radius ( $r_1$ ) ..... 21b, 27-37a, 42o  
 34<sup>2</sup> A row of setulae on lower side of 1<sup>st</sup> radius ( $r_1$ ) ..... 74b  
 34<sup>3</sup> First radius ( $r_1$ ) ends outwards of the middle of wing ..... several Sciomyzidae and at least 88g  
 35<sup>1</sup> Vein  $r_{2+3}$  strongly bent upwards to costa, ending very near to  $r_1$  ..... 64a  
 35<sup>2</sup> Veins  $r_{4+5}$  and  $m_{1+2}$  towards tips convergent ..... 24a, 25a, 38a, 42c, 76b, 85  
 35<sup>3</sup> Costa ends at tip of  $r_{4+5}$  ..... 42c  
 35<sup>4</sup> Wing tip moderately acute, similar to some extant Camillidae ..... 4i, 5b  
 35<sup>5</sup> The densely arranged short setulae along costa only present until tip of  $r_{2+3}$  ..... 87  
 35<sup>6</sup> Costal spinules along costa ending at tip of  $r_{2+3}$  ..... 36a  
 36<sup>1</sup> Subcosta bent up in an angle of about 90°-100° towards costa-break ..... 17e, 25, 40e, 42f  
 40<sup>1</sup> A basal costal break outwards of the humeral crossvein (seems to be) present ..... 5b, 5 l, 6a, 8,  
      ..... 19h, (88h), 89  
 41<sup>1</sup> Posterior crossvein (tp) absent ..... 42c  
 41<sup>2</sup> Basal crossvein (tb, separating discal cell and second basal cell) absent ..... 17a, 32, 32a, 32b, 69  
 42<sup>1</sup> Anal cell and anal vein ( $A_1+CuA_2$ ) absent or rudimentary (cell open distally) .. 0a, 5c, 6, 6a, 25a, 32,  
      ..... 40h, 41a, 42a, 52c, 72a (weak in 5b, 5 l)  
 42<sup>2</sup> Anal cell ending acute or produced into a short acute lobe at posterior corner ..... 2a, 2b, 2c,  
      ..... 2d, 21b, 37a, 76b, 80, 80a  
 42<sup>3</sup> Alula (soft basal separated hind part of wing) very small or absent ..... 5b, 5 l, 5i, 6a, 25a  
 42<sup>4</sup> Lower calypter (at base of wings) with 4 stiff parallel spines along its fringe ..... 78d  
 44<sup>1</sup> Dense long pubescence around posterior spiracle ..... 88i  
 45<sup>1</sup> One or 2 pairs of well developed scapulars on mesonotum towards back of head ..... at least 19d, 78d  
 46<sup>1</sup> Face (= praefrons) above clypeus and mouth margin convex ..... 5k, 5 l, 49i  
 46<sup>2</sup> Face with deep foveae for inserting the 3<sup>rd</sup> antennal segments ..... 32, 43b, 43c, 52, 56  
 47<sup>1</sup> Gena (= cheek plus jowl) below eye completely absent ..... 25a, (79i), 88g  
 48<sup>1</sup> Proboscis sclerotized, short labellum bearing rasping teeth ..... 79a  
 48<sup>2</sup> Proboscis elbowed with narrow and partly prolonged labellum, each side with  
      an acute free tip ..... 32, 52c, 52d, 52e  
 49<sup>1</sup> Above each 1<sup>st</sup> antennal segment (scape) a narrow transverse sclerite, ptilinal fissure flat ..... 88i  
 49<sup>2</sup> The 1<sup>st</sup> antennal segment rudimentary, hidden under the well developed 2<sup>nd</sup> one ..... 16h, 25a  
 49<sup>3</sup> The 2<sup>nd</sup> antennal segment with many strong proclinate bristles, upright ones absent ..... 49c, 58, 73  
 49<sup>4</sup> The 2<sup>nd</sup> antennal segment with central triangular projection at outer surface,  
      rarely on inner side ..... 19a, 42, 42b, 42e, 42g, 73a, 79f, 87  
 49<sup>5</sup> The 2<sup>nd</sup> antennal segment cap-like covering the 3<sup>rd</sup> ..... 6a, 49c, 54b, 58, 73  
 49<sup>6</sup> The 3<sup>rd</sup> antennal segment ball-like, nearly as thick (broad) as long and high ..... 52c, 78d, 79d  
 49<sup>7</sup> Third antennal segment exceptional large ..... 16b, 21, 61  
 49<sup>8</sup> Third antennal segment small or very small ..... 11d, 17d, 19b, 19c, 21, 21b, 40h, 42a, 49f, 49h, 59b  
 49<sup>9</sup> Pectinate arista ..... 4, 40, 40c, 40f, 49c, 54a, 73  
 49<sup>10</sup> Long pectinate arista,  $f_2$  and  $f_3$  thickened, with spinules ..... 84a  
 49<sup>11</sup> Arista absent or vestigial ..... 49b, 61  
 49<sup>12</sup> Arista inserting on terminal edge of 3<sup>rd</sup> antennal segment ..... 33b, 42a, 73a, 74, 74b, 74e, 79d  
 49<sup>13</sup> Arista broadened in distal part (its 3<sup>rd</sup> segment) ..... 2a, 2b  
 49<sup>14</sup> Arista bare, its very base knob-like thickened ..... 4a  
 51<sup>1</sup> With a nearly or completely closed conical oviscape around ovipositor ..... 15, 16, 16a, 17a, 40, 43c,  
      ..... 49, 49e, 50, 56, 66, 68, 69  
 51<sup>2</sup> Last sternite or pleuron between 6<sup>th</sup> tergite and 6<sup>th</sup> sternite with a simple or complicated sclerotized appen-  
      dix in male, if simple it bears a long bristle ..... 40a, 60b, 66  
 51<sup>3</sup> Epandrium or tergite or "pseudotergite" in front of it with peculiar structures or bristles (surstyli and cerci  
      neglected) ..... 40g, 45a, 47, 49e, 79g, 88c, 88d, 88g  
 51<sup>4</sup> Epandrium (partly together with 6<sup>th</sup> tergite) movable separated and bent downwards ..... 16 l, 19h,  
      ..... 21a, 40a, 74a, 74b, 88g  
 51<sup>5</sup> Long "pseudotergite(s)" [HENNIG: "Ringe"] in addition to 6<sup>th</sup> tergite in front of  
      large epandrium ..... 19h, 37, 79f, 84

51 <sup>6</sup>	Large-scaled male cerci, these with long hairs and as long as or longer than surstyli . . . . .	32, 79f
51 <sup>7</sup>	Male cerci ball-like . . . . .	88c
51 <sup>8</sup>	Female cerci fused as a tip of a piercing ovipositor . . . . .	16, 40, 49, ?56
52 <sup>1</sup>	The fly is pitch-black . . . . .	70 b; in addition also wings are pitch black . . . . .
52 <sup>2</sup>	Head distinctly broader than thorax . . . . .	1, 1a, 5b, 5k, 5 l, 17d, 25a, 40d, 49i
52 <sup>3</sup>	Head distinctly higher than long . . . . .	17a, 40, 54, 58, 73
52 <sup>4</sup>	Mesonotum with 5 black stripes on yellow ground like many extant Chloropidae . . . . .	32c, 72a, 74a
52 <sup>5</sup>	Mesonotum moderately flattened . . . . .	24a
52 <sup>6</sup>	A slight groove around hind corner of mesonotum (similar to Calyptratae) present . . . . .	2d

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- 0a [Not all characters visible for a placement in key]. Male: huge epandrium, anal cell absent, small species; vi, f<sub>1</sub> with ventral spine, all t with a dpr, long palpi, thick labellum, arista normal . . . . . sp.n. 1
- 0b Metatarsus of hind leg peculiarly shortened and slightly thickened, arista thin and long, bent sideways, tiny fly (specimen seen by M.v.T., possibly lost) . . . . . Sphaeroceridae
- 1 (2) Eyes on short stalks (I, fig. 43) . . . . . *Prospryracephala succini* (LOEW), Diopsidae
- 1a "Bulldozer"-head much wider than thorax, wider than long; compare also 24a. Go to 5b, 5l.
- 1b Eyes on long stalks . . . . . sp.n. 2, Diopsidae
- 2 (1) Eyestalks absent.
- 2a Anal cell long, its acute tip petiolate (not reaching wing edge), 3 ors, arista normal, at most 4 st, ia absent . . . . . *Palaeomyopa tertaria* MEUNIER, Conopidae
- 2b Anal cell and ors as in 2a, arista broadened distally at "dorsal and ventral" side [the description does not mention to which side the arista of *P. tertaria* is widened]; vte and vti, 7 st, 1 bristle between sa and ipa (= ia) [STUKE 2003: 95 in German: "2<sup>nd</sup> sa" and "between humerus and transverse suture opposite to his figure 1"] . . . . . *Palaeomyopa hennigi* STUKE, Conopidae
- 2c Anal cell as in 2a, 2 ors, femora thickened and hairy, 0 st . . . . . *Hoffeinsia baltica* STUKE, Conopidae
- 2d Anal cell as in 2a, vi, ors, vte, vti, h, pp, m, st, dc, prsc, ia (together 11 bristles) all absent, 3 weak notopleural bristles in an oblique row (anterior end low, posterior high), 2 bristles between wing base and scutellum (probably epa and ipa), furthermore mesonotum bare, scutellum with 1 ap and 1 la, each divergent from the adjacent bristle, peculiar tip crossvein m<sub>1</sub> between r<sub>2+3</sub> and r<sub>4+5</sub> present, a slight groove around hind corner of mesonotum (similar to Calyptratae) present, front edge of frons as a lobe covering mid of lunule, body 4.24 mm . . . . . sp.n. 3, Conopidae
- 3 (10) Anterior fronto-orbital bristle (ors) directed forwards (proclinate), inserted about half distance between vertex and front edge of frons (I, fig. 292). Postvertical bristles (pvt) always convergent.
- 4 (5) In addition to the single proclinate ors two strong reclinate fronto-orbital bristles present (I, fig. 308, 309). One pair of prescutellar bristles (prsc) present (I, fig. 311, 312). Arista long, pectinate on upper and lower sides (I, fig. 310). Costa with spinules, sc is a fold, r<sub>4+5</sub> bent backwards . . . . . *Electrophortica succini* HENNIG, Drosophilidae
- 4a Arista completely bare (naked) with very short swollen basal segments, inside of the 2<sup>nd</sup> ors and near the large ocellar triangle a long proclinate ors on widened orbits, head distinctly broader than thorax (76:60), face receding towards mouth margin; 3+1 dc, prsc absent, very short and weak costal spinules with only 3 interjacent microchaetae, sc complete, ending far from r<sub>1</sub>, axillaris stronger and longer than the short analis, eye oblique, body/wing 2.49-2.74/2.44-2.45 mm. Family known from extant species in the Afrotropical region, amber species in all details identical, but surstylus seems not fused with epandrium . . . . .
- . . . . . sp.n. 4, *Natalimyza* BARRACLOUGH & MCALPINE, Natalimyzidae.
- 4b Clypeus prominent, 2 dc, the anterior dc much smaller, long prsc present, 10 acr-rows, 1 la, 1 ap, at least t<sub>2</sub> and t<sub>3</sub> with dpr, arista with short sparse rays, wing 2.5-3.3 mm . . . . .
- . . . . . sp.n. 5, ?*Electrophortica*, Drosophilidae
- 4c Arista only with short pubescence; 1 ap, 1 la, sc distally reduced . . . . .
- . . . . . sp.n. 6, ?*Electrophortica*, Drosophilidae
- 5 (4) In addition to the proclinate ors only 1 strong reclinate ors present. (I, figs. 286, 291, 292, 298, 299). Prescutellar bristles (prsc) absent. Arista with prominent pubescence but without long rays.
- 5a Spinules on costa absent, 3<sup>rd</sup> antennal segment round; 2 st, prsc, ia, sc ends far from r<sub>1</sub> . . . . . sp.n. 7

- 5b Head very short, much broader than thorax, at the ratio of 3:2, pedunculate eyes ( $\sigma$ ) on short stalks, probably sexual dimorphic,  $f_1$  at lower side with strong\* [\* see comment below] medial black thorn within a row of 6 weak bristles; vi, 2 ors, long divergent oc, convergent pvt, vte, vti, h, 2 n, prs, mesopleuron with 12-14 evenly scattered\* hairs, 0 m, 2 st, 2 dc, prsc, epa, ipa, sa\*, 6 acr-rows, la, ap,  $r_{4+5}$  ends at wing tip, wing tip slightly acute\*; spinules on costa absent; pvt convergent,  $f_2$  with 1 anteroventral bristle\* in distal quarter,  $f_3$  with 1 anterodorsal bristle\* in last quarter, all t with dpr,  $t_3$  without\* a ventral preapical bristles,  $t_1$  with several combs of microsetulae at inner end, costal spinulae absent, subcostal break near to  $r_1$  with two bristles, of 2 ors, 2 st, 2 dc, prsc, sc weak ends at subcostal-break near  $r_1$ , length of 3<sup>rd</sup> antennal segment nearly two times its height, all tibiae with dpr, anal cell and anal vein vestigial, arista with long pubescence (or very short pennate), face flat\*, wing 2.54 mm. Compare couplet 5 l, a very similar or possibly conspecific species! Differences are marked here by an asterisk ..... *Protocamilla* sp., Camillidae
- 5c 1<sup>st</sup> metatarsus (mt<sub>1</sub>) with a long bristled lobal appendix, clypeus prominent; pvt crossed, 2 pp (anterior one longer), mesopleuron with hairs, 4 m, 2 st, 2 dc, prsc, 0 ia, 1 ap, 1 la, costal spinules absent, sc a fold towards the coastal-break near to  $r_1$ , anal cell rudimentary, 3<sup>rd</sup> antennal segment 1.5 times longer than high and with long pubescence, wing 2.01 mm ..... sp.n. 8
- 5d Go to 54a.
- 5e As 5c but mt<sub>1</sub> normal, 1 m, 3 st,  $r_1$  short and ending in the basal third of wing ..... sp.n. 9
- 5f Similar to 5e, 0 m, 3 st,  $r_1$  short, ending in the basal third of wing ..... sp.n. 10
- 5g Very small (wing 1.64 mm), wing tip slightly acute and at  $r_{4+5}$ ;  $f_1$  with a spine on lower side; 1 st, prsc, 0 ia, sc ends near to  $r_1$ , 3<sup>rd</sup> antennal segment longer than high ..... sp.n. 11, Camillidae
- 5h Vein  $r_1$  ends far distally in mid of wing, no costal-break, vi absent; 1 pp, 0 m, 2 st, 3 dc, long prsc, at least  $t_1$  and  $t_2$  with a dpr, arista bare, vein axillaris prominent, gena as high as 3<sup>rd</sup> antennal segment, female cerci seem to be sclerotized and bent upw ards at their very ends, wing 3.12 mm ... sp.n. 12, ?Campichoetidae
- 5i Small species (wing 1.96 mm), wing tip moderately acute, alula absent; vi, pvt crossed, 1m, 1 st, 2 dc, short prsc, 1 la, 1ap (both crossed),  $f_1$  with spine on lower side, costal spinules distally of subcostal break absent (basally only bristles are present), sc vestigial ..... sp.n. 13, Camillidae
- 5k Face convex, head broader than thorax, vertex saddle-like, clypeus prominent, prsc absent, anterior ors nearer to eye than posterior, a tiny setula between both; oc minute, 0 h, 0 pp, 0 m, 2 st, 1 dc,  $f_1$  with a row of 14 ventral bristles, all t without dpr,  $t_1$  at inner side with cleaning comb, body 2.8 mm ..... *Procyamops succini* HOFFEINS & RUNG, Periscelididae
- 5l "Bulldozer head" and habitus as in couplet 5b; differences: face with a central swelling, 2 prs,  $f_1$  with a central strong ventral bristle instead of a thick thorn, 1 h, 1 prs, 2 n, 1 row of mesopleural setulae, 1 sa present, more than 6 strong bristles at hind edge of 6<sup>th</sup> tergite, body 2.4 mm ..... *Protocamilla groehni* GRIMALDI, Camillidae
- 6 (7) Mesopleuron setulose. Sternopleuron with setulae and 3 sternopleural (st) bristles present at upper margin (I, fig. 300). No spinules along costa, anal cell rudimentary ..... *Protocamilla succini* HENNIG, Camillidae
- 6a Tiny species (body/wing 1.84/1.96 mm), clypeus convex covering mouth opening across from side to side, dorsal bristle on 2<sup>nd</sup> antennal segment peculiarly bent forwards, face convex, anal cell and anal vein absent; pvt proclinate-divergent, occiput concave; 0 h, 1 dc, 0 prsc, each side 4 la (the basal one longest), ap widely separated, scutellum longer than wide, two costal breaks, ta far basal on discal cell, 3<sup>rd</sup> antennal segment longer than high with long pubescence, 2<sup>nd</sup> segment cap-like covering the inner side of the 3<sup>rd</sup> ... sp.n. 14, ?Aulacigastridae or ?Periscelididae
- 7 (6) Mesopleuron bare. Upper margin of sternopleuron with 2 sternopleural bristles only (I, fig. 288, 294).
- 8 (9) 3<sup>rd</sup> antennal segment curltly two times as long as broad (= high) (I, fig. 292). Spinules along costa, costa is weak distally of humeral crossvein ..... *Pareuthychaeta minuta* (MEUNIER), Campichoetidae
- 9 (8) 3<sup>rd</sup> antennal segment only 1.5 times as long as broad (= high) (I, fig. 286). Spinules along costa are present ..... *Pareuthychaeta electrica* (MEUNIER), Campichoetidae
- 9a Spinules along costa absent, oval 3<sup>rd</sup> antennal segment with long pubescence (arista with normal or elongate pubescence), 0 m, 2 st, 2 long dc, 0 prsc, at least  $t_1$  and  $t_2$  with a dpr,  $t_1$  with cleaning comb, sc as a fold towards costa-break near  $r_1$ , genae very narrow, wing 2.93 mm ..... sp.n. 15, ?Pareuthychaeta, Campichoetidae
- 10(3) Lower fronto-orbital bristle not proclinate.

- 11(20) Also in front of the transverse suture of mesonotum one or two pairs of presutural dc present; consequently there are altogether 4 (I, fig. 161; II, fig. 6; III, fig. 14) or 5 (I, fig. 193, 203) or 6 dc present; go also to amendments of couplet 91.
- 11a 7 ors, scutellum with hairs ..... sp.n. 16
- 11b 4+2 dc, tiny species; go to couplet 17a.
- 11c 3+2 dc, 4 ors ..... sp.n. 17
- 11d [Number of dc not observable], 3 ors, 1 h, 3<sup>rd</sup> antennal segment small, no costal-break ..... sp.n. 18
- 11e [Number of dc not observable], small species, each side 2 vi ..... sp.n. 19
- 11f [Number of dc not observable], femora thick with spiny bristles on lower side ..... sp.n. 20
- 11g 9 + 6 dc, the posterior 1<sup>st</sup> dc slightly longer and stronger than the long row of weak anterior ones; head broader than thorax,  $r_{3+4}$  and  $m_{1+2}$  convergent; go to couplet 25a.
- 11h 4 + 1 dc, all t with an uncommonly rich equipment of long bristles (Fig. 12), antennae bent downwards, 2<sup>nd</sup> article with small dorsal seam and without outstanding bristles, but with "tufts" of short setulae, 3<sup>rd</sup> antennal segment only slightly longer than 2<sup>nd</sup>, vi shorter than the 3-4 strong and inclinate peristomal bristles, 2 ors, the anterior one bent backwards and slightly outwards, ptilinal suture not curved but straight; long divergent oc, if in 2-3 irregular rows, pvt long (possibly parallel or convergent), vte, vti, h, 2 n, 1+1 pp (posterior stigmatal bristle  $\frac{1}{4}$  length of anterior proepisternal), prs, 0 m, 2 st, mesopleuron and sternopleuron without hairs, prsc, 0 ia, epa, ipa, sa, subcostal break, sc complete, ending near to  $r_1$ ,  $r_1$  bare, cheeks narrow, body/wing 4.7/4.1 mm ..... sp.n. 21, ?Piophilidae
- 12(17) Only 3 postsutural dc present (I, fig. 161; II, fig. 6; III, fig. 14). Here also Pseudopomyzidae with spinules along costa and 3+1 dc must be considered, go to 17.
- 13(16) Intra-alar bristle present (ia: I, fig. 161; III, fig. 14). Inner and outer vertical bristles [in original key erroneously "pairs"] present (vti and vte; I, fig. 159, 160; III, fig. 8, 10).
- 14(15) On each side 3 reclinate ors present (III, fig. 8, 10). Subcostal vein and  $r_1$  ending in costa far from each other (III, fig. 17). Sternopleuron near upper margin with 2 very long and strong st (III, fig. 15). Large species (6,5 mm). Wing 5.23-7.33 mm. Scutellum with long la and short ap. Go to also to 48a. ....
- ..... *Proneottiophilum extinctum* HENNIG, Proneottiophilidae
- 14a Intra-alar present, 3 reclinate ors, sc ends near to  $r_1$  ..... sp.n. 22
- 14b 4 reclinate ors, 1 ia, la much longer than ap; vi, 1 h, 0 m, 1 st, 0 prsc, 2 rows of acr, all t with dpr, complete sc ends far from  $r_1$ , subcostal break, wing 6.48 mm ..... sp.n. 23, *Proneottiophilum*, Proneottiophilidae
- 14c 2 reclinate ors, 1ap, 1 la, prsc, 1 st ..... sp.n. 24
- 15 (14) 2 reclinate and 1 inclinate ors present (I, fig. 159); sc and  $r_1$  ending relatively close together (I, fig. 162A). Sternopleuron with 1 strong and 4 weak st at upper margin (I, fig. 156); pvt divergent, 1 pp, 0 m, 4 st, prsc, 1 ia, small species (2.5 mm) ..... *Protodinia electrica* HENNIG, Odiniidae
- 16 (13) Intra-alar bristles absent, 1 vertical bristle only (vte?; II, fig. 3), 1 h and 1 pair of scutellar bristles (ap) (sc; II, fig. 6) present ..... *Pallopterites electrica* HENNIG, Pallopteridae
- 16a Oviscape and ovipositor typical for Pallopteridae, vte and vti, ap and la, meso- and sternopleuron with hairs,  $f_2$  and  $f_3$  with 1 anteroventral bristle, costal spinules absent. Compare also couplet 19a-e .....
- ..... sp.n. 25, ?Pallopteridae
- 16b Large 3<sup>rd</sup> antennal segment axe-formed, angulated above, ia absent, 1 anteroventral bristle on  $f_2$ , costa without spinules ..... sp.n. 26, ?Sciomyzidae
- 16c Similar to 16a, but costal spinules present ..... sp.n. 27
- 16d vi, 3 ors, vte and vti; ia and prsc absent, costal spinules present, 1 strong  $f_3$  bristle ..... sp.n. 28
- 16e 2 ors, vte and vti, all femora bristled ..... sp.n. 29
- 16f 1 ors, 5+1 dc, prsc absent, spinules on costa present ..... sp.n. 30, Heleomyzidae
- 16g 1 ors, 3+1 dc, prsc, costal spinules are absent ..... sp.n. 31
- 16h 3 ors present, vertex saddle-shaped (concave), 1<sup>st</sup> antennal segment rudimentary; all following bristles absent: vi, pvt, prs, m, st, prsc, ia, ipa, and costal spinules, sc ends far from  $r_1$  ..... ?Sciomyzidae, sp.n. 32
- 16i 3 ors, the anterior bent inwards, small orbital setulae bent backwards, pvt divergent, female with short oviscape (conical sclerotized protection of ovipositor around tip of abdomen); 1 pp, 0 m (1 specimen in one side: at hind edge 1 m, teratological?), 1 + 3 st, sc ends near  $r_1$ , small species. Very similar to extant Agromyzidae, but epandrium movably attached, oviscape can be partly drawn in, mesopleural bristle absent. Go to couplet 15.
- 16k 3 ors, the anterior bent inwards, orbital setulae and m absent ..... sp.n. 33



**Fig. 5:** Sciomyzidae, Phaeomyiinae, undescribed species, ♀, body 6.8 mm (measured without the telescopic ovipositor), lateral habitus, details of frons partly obscured by syn-inclusions; coll. HOFFEINS 1655-1.

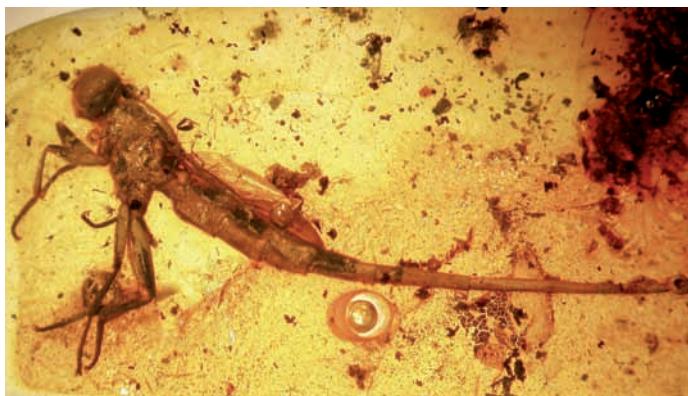


**Fig. 6:** Cypselosomatidae, *Cypselosomatites succini* HENNIG, ♀ and ♂ in copula (♀ at left), body of female about 5.7 mm, dorsal habitus; evidence of sexual dimorphism in size occurring in this family. Female with phoretic pseudoscorpion which itself is occupied by phoretic mites; the mating pair was "diving" with its frontal part into the liquid resin; coll. HOFFEINS 1285-3.



**Fig. 7-8:** Megamerinidae, *Palaeotanypeza spinosa* HENNIG, ♂, body 9.0 mm; ventrolateral habitus with remnants of vivid colour pattern on legs and body; details of male genitalia and hind femora; coll. HOFFEINS 1656-2.





**Fig. 9:** Megamerinidae, *Palaeotanypeza* sp., ♀, body 7.6 mm, ovipositor 9.1 mm, lateral habitus; coll. HOFFEINS 1656-1.



**Fig. 11:** Natalimyzidae, *Natalimyza* sp., ?♀, body 2.8 mm, dorsal habitus, coll. HOFFEINS 877-1.



**Fig. 10:** ?Sciomyzidae, undescribed species, ♀, body 5.2 mm, lateral habitus; evidence of viviparity in Eocene; note the 8 emerged larvae; coll. HOFFEINS 1522-1.



**Fig. 12:** ?Piophilidae, undescribed species, ♂, body 4.4 mm, lateral habitus, coll. HOFFEINS 1374-1.



13

**Fig. 13-14:** Pallopteridae, *Glaesolonchaea* sp., ♀, body 3.0 mm; ventral habitus and the typical lonchaeid/pallopterid oviscape; coll. HOFFEINS 966-7.



14

- 16l Tiny species, wing 1.88 mm, vi, 4 ors, pvt convergent, a pair of scapulars, 1 pp, 0 m, 1 st, prsc, 0 ia, scutellum small with 3 pairs of bristles: 1 long on disc of scutellum, 1 short la, 1 long ap, all t without dpr, sc ends as fold near  $r_1$ , subcostal-break, epandrium bent down, with acute surstyli ..... sp.n. 34
- 16m Clypeus prominent, lower hind part of eye retreating, h, m, prsc and ia all absent; vi, 1 ors, pvt convergent, 3+1 (or 4+1) dc, 1 st,  $t_1$  and  $t_3$  with,  $t_2$  without dpr, costa with spinules, wing 3.56 mm ..... sp.n. 35
- 16n 2 reclinate ors (anterior one shorter), long oc, pvt crossed, 2 well developed pp, mesopleuron without hairs, 0 m, 2 st, prsc, 4-6 acr-rows, 1 la, 1 ap, all t with dpr, costal spinules, subcostal cell long, subcostal break, analis long, axillaris present, male with one pair of prolonged "dististyli", body/wing 4.15/4.35 mm, [ia not mentioned in original description; holotype checked: absent] ..... *Protoorbellia hoffeinsorum* WoźNICA, Heleomyzidae
- 17(12) 4 [or 3-5] postsutural dorsocentral bristles (dc; I, fig. 193, 203) present.
- 17a (17b) Key of HENNIG 1971: Each side 4 ors present ... *Eopseudopomyza kuehnei* HENNIG, Pseudopomyzidae
- 17b (17a) Ditto: Each side only 1 or 2 ors present. Go further to couplet 18.
- 17c 6-8 postsutural dc, 2 h!; 3 ors, pvt parallel, prsc, 1 ia, large species ..... sp.n. 36
- 17d Tiny species, wing 1.23 mm, 4+2 dc, vi, ors, vti and la all absent, possibly also anterior crossvein; oc long, 1 h, probably only 1 anterior n, 1 m, only 2 rows of acr, each consisting of only 3 setulae, head broader than thorax, 3<sup>rd</sup> antennal segment small, arista long ..... sp.n. 37
- 17e Subcosta strongly bent towards costa; vi and prsc absent, 1 ors, 1 h, prs ..... sp.n. 38
- 18 (19) Each side with only 1 ors (I, fig. 194); h absent, costa with spinules, robust femora, especially in males (sexual dimorphism),  $t_1$  with long dpr ..... "Suillia" major (MEUNIER), Heleomyzidae
- 19 (18) Each side with 2 ors (I, fig. 202). Costa with spinules ... *Protosuillia media* (MEUNIER), Heleomyzidae
- 19a 2 ors, 2<sup>nd</sup> antennal segment at inner side prolonged as a spine onto 3<sup>rd</sup> antennal segment. 3<sup>rd</sup> antennal segment large, 4+2 until 6+2 dc ..... sp.n. 39
- 19b 4 ors, pvt convergent, prsc present. 3<sup>rd</sup> antennal segment small, embedded in 2<sup>nd</sup> one; 3 st, 3 la. Species runs also to couplet 16. Go to couplet 17a.
- 19c 2 ors, 3<sup>rd</sup> antennal segment small ..... sp.n. 40
- 19d 2 ors, a pair of "prescapulars" on front thorax towards head, 3<sup>rd</sup> antennal segment "big", after the photo we judge it as normal; 1 pp, 2 m, 4+(1-2 small) dc, prsc, 1 st, all t with dpr,  $f_2$  with 1 "anterior" (anteroven-tral?, anterior never seen in acalyptates) bristle, costal spines, wing 2.1 mm ..... *Paleoheleomyza kotejai* WoźNICA & PALACZYK, Heleomyzidae
- 19e Judgement of presutural dc difficult, 2 dc behind, 7+5 anterior small). Go to couple 78 d.
- 19f 4 ors, 3<sup>rd</sup> antennal segment normal, vi and prs both absent, 4+1 dc, the two foremost ones small, ia present; 1 pp, pvt divergent, 1 h, 2 n, 2 st, prsc, sc complete, no costal-breaks, large species ..... sp.n. 41
- 19g ia, m, costal spinules all absent, vi, 2 ors, 5+1 dc, pvt parallel; vte, vti, h, 2 n, prs, pp, 3 st, all t with dpr, sc ends far from  $r_1$  ..... sp.n. 42
- 19h 3 ors, 4+2 dc, mid leg of male with strongly broadened 2<sup>nd</sup> and 3<sup>rd</sup> tarsomere, long and thin arista, sc rudimentary, costa with humeral- and subcostal break, epandrium with prominent pregenital segment behind 6<sup>th</sup> tergite movable, bent downwards, body/wing 2.40/2.15 mm ..... sp.n. 43
- 20 (11) Dorsocentral bristles (dc) present only behind transverse suture.
- 20a Frons with a row of at least 10 very short ors, 1 very short dc, proboscis long. Go to 32.
- 20b As 20a, but proboscis short. Go to 72a.
- 21 (22) Pteropleuron with strong bristles (I, fig. 110). (3<sup>rd</sup> antennal segment uncommonly enlarged, compare also couplet 16b) (I, fig. 106-108) ..... *Palaeoheteromyza crassicornis* MEUNIER, Sciomyzidae
- 21a 3<sup>rd</sup> antennal segment normal, 2 ors, 2 dc; 3 pteropleurals, pvt parallel-divergent, pp, m and st both absent, prsc, all t with dpr, small evenly arranged costal spinulae,  $r_1$  bare, subcostal cell sclerotized and darkened, 6<sup>th</sup> tergite and epandrium bent down, wing 3.17 mm ..... sp.n. 44, ?Sciomyzidae
- 21b Large species, wing 4.00 mm, 3<sup>rd</sup> antennal segment small, round, 2 ors, 2 dc, costal spinules absent; vi, pvt divergent, prs, 3 pteropleurals, 1 long pp, 1 st, long convergent prsc, 0 ia, at least  $t_1$  and  $t_3$  with dpr,  $r_1$  with setulae above, costal break absent, anal cell with very short point, large affiliated surstyli ..... sp.n. 45
- 22 (21) Pteropleuron bare (3<sup>rd</sup> antennal segment not exceptionally enlarged).
- 23 (26) Only 1 notopleural bristle (n) present (I, fig. 39, 65, 66).
- 24 (25) Postvertical bristles (pvt) absent (I, fig. 41). Hind femora strongly thickened and on lower side with 2 rows of spines (I, fig. 39). Costa without a break (I, fig. 42) ..... *Palaeotanypeza spinosa* MEUNIER, Megamerinidae

- 24a Hind femora normal, 3<sup>rd</sup> antennal segment tiny, eye oblique, extremely different in both diameters, vertex saddle-shaped, mesonotum flattened behind; 1 ors, 0 h, 0 m, 1 dc, dc and ap upright, la absent, sc absent, no subcostal break, bristle or spine on  $f_1$  absent, mt<sub>1</sub> thickened and matt, thicker than tibia, r<sub>4+5</sub> and m<sub>1+2</sub> convergent, clypeus only linear, body/wing 1.9/1.71-1.91 mm ..... sp.n. 46, ?Periscelididae
- 25 (24) Postvertical bristles present, divergent (I, fig. 61-64). Hind femora not thickened (I, fig. 60). Costa with distinct break (I, fig. 67), sc as a fold in a 90°-angle towards break, male with 2, female with 3 pairs of scutellars, one on the disc ..... *Electrochyliza succini* HENNIG, Psilidae
- 25a Postverticals tiny, proclinate and parallel or slightly divergent, head broader than thorax, r<sub>3+4</sub> and m<sub>1+2</sub> convergent, mesonotum without any pubescence, brilliantly shining with only 3 rows of casually inserting setulae, one unpaired central and each side one in front of the 1<sup>st</sup> weak dc, those setulae in front of 1<sup>st</sup> dc (8 behind and 6 in front of transverse suture, compare couplet 11g) may be counted as dc; anal cell only a rudiment, alula ditto; tiny vi, 5-6 very weak ors, very short, weak, proclinate oc, long vte and vti, 0 h, meso- and sternopleuron brilliantly shining without hairs or bristles, 1 la, ap, all t without dpr, r<sub>1</sub> with one setula above at height of costal break, sc distally reduced, eyes large, cheeks absent below eye, body/wing 1.91/1.96 mm ..... sp.n. 47, Asteiidae
- 26 (23) 2 notopleural bristles or more (compare 78d) present (e.g. I, fig. 83, 84; III, fig. 23).
- 26a Try also couplet 79.
- 27 (38) Distal part of r<sub>1</sub> with spinules/setulae on upper side (I; fig. 73, 85, 93, 178, 316; III, fig. 24). In couplets 32, 32a, 32b, 32c partly only 2, which are very difficult to detect, observe wing profile.
- 28 (31) Mesopleuron setulose and with 1-2 relative long and strong bristles along hind edge (I, fig. 83, 175, 177). Postvertical bristles always divergent (I; fig. 81, 166-169).
- 29 (30) Prescutellar [presutural is a mistake in HENNIG] bristles present (I, fig. 83, 84). Each side 4 fronto-orbital bristles present (I; fig. 81, 82). Posterior spiracle with a characteristic group of setulae (I, fig. 83A). Larger species (7 mm). No costal break, prs absent ..... *Protorygma electricum* HENNIG, Sepsidae
- 29a Posterior spiracle with 1 bristle, a small prs is present, 7 ors ..... sp.n. 48
- 29b Vibrissa, 7 ors, prs and costa-break are present, sc as a fold only ..... sp.n. 49
- 29c Posterior spiracle bare, 7 recurved ors, typical anteroventral bristle on f<sub>2</sub>, body 5-6 mm ..... sp.n. 50
- 30 (29) Prescutellar bristles present and presutural bristle absent (I, fig. 174-177). Each side only 3 fronto-orbital bristles (ors: I, fig. 166-169). Posterior spiracle without a group of setulae, but a feathery crown of tiny hairs is present. Arista with long pubescence, smaller species (4-4,5 mm) ..... *Acartophthalmites tertaria* HENNIG, Acartophthalmidae
- 31 (28) Mesopleuron bare, even at hind margin without bristles.
- 32 (33) Postvertical bristles (pvt) convergent (I, fig. 314). Labellum of the proboscis elongate (I, fig. 315). Distinct fronto-orbital bristles absent (I, fig. 314, 315). Mesonotum without presutural bristle (prs) and with just one pair of dorso-centrals (dc: I, fig. 318), prsc present. Scutellum with 4 or more small bristles on each side (I, fig. 318) or lateral bristles small like dorsal ones. Antennae dark. 3 longitudinal moderately impressed grooves on mesonotum. [Variation: see 32a and text] ... *Protoscinella electrica* HENNIG, Chloropidae
- 32a Similar to couplet 32 and the figs. in HENNIG but in variable combinations: oc missing, only few setulae on r<sub>1</sub>, prsc absent, ipa present, only 1 short sa bristle instead of a group, elongate la absent. Compare discussion in text and 72a ..... Preceding species
- 32b Similar to couplets 32 and 32a but 3<sup>rd</sup> antennal segment much smaller than in HENNIG I, fig. 214, proboscis and palpi shorter than in couplet 33, 4 prsc in line ..... sp.n. 51, *Protoscinella*, Chloropidae
- 32c Similar to 32 and 32a but 3<sup>rd</sup> antennal segment and palpi yellow and very thick, proboscis short, 5 black stripes on light ground of mesonotum. Go to 72a.
- 33 (32) Postvertical bristles diverging (I, fig. 70, 89). Labellum of proboscis not elongate. On both sides 2 or more strong fronto-orbital bristles present (ors: I, fig. 70, 89; III, fig. 22). Mesonotum with 3-5 dc [couplet 36a only 2 dc] and 1 – sometimes weak – presutural bristle (I, fig. 72, 91, 92; III, fig. 23). Scutellum each side with only 2 or 3 bristles (I, fig. 72, 91, 92; III, fig. 23).
- 33a Only 3 setulae on r<sub>1</sub>, face concave, prs absent, 2 dc; vi absent, 2 strong ors, oc short, divergent-proclinate, pvt convergent-parallel-, 0 m, 1 st, 0 prsc, 8-10 rows of acr, sc complete, wing 2.01 mm ..... sp.n. 52
- 33b 3<sup>rd</sup> antennal segment shorter than high, arista terminal, bent backwards, 2 ors, 2 dc; first cross vein far basal, wing 1.96 mm ..... sp.n. 53, ?Clusiidae

- 34 (35) Each side 4 pairs of strong fronto-orbital bristles present (III, fig. 22). Scutellum with 3 bristles on each side (III, fig. 23). Wing with a subcostal break (III, fig. 24) ..... *Electroclusiodes radiospinosa* HENNIG, Clusiidae
- 35 (34) Each side only 2 strong fronto-orbital bristles present (ors: I, fig. 70, 89). Scutellum with 2 pairs of bristles (I, fig. 72, 91, 92). Wing without a subcostal break (I, fig. 73, 93).
- 36 (37) Upper margin of sternopleuron with 3 long and strong sternopleural bristles (I, fig. 91, 92). Mid tibia at hind margin and hind tibia above the dpr with some small bristles (I, fig. 94) ..... *Prophaeomyia loewi* HENNIG, Sciomyzidae
- 36a Large species, body/wing of ♂ 9,8/9,7 mm, 1 ors, 4-5 st, costal spinules end at  $r_{2+3}$ ; oc long, pvt long and divergent, vte, vti, 1 h, 2 n, prs, 1 pp + 2-3 weaker setulae near pp, 0 m, 2 dc, epa, ipa, sa, la, ap,  $f_1$  with strong dorsal and ventral bristles,  $f_2$  with weaker bristles: 1 dorsal + 2 ventral ones,  $f_3$  with several bristles in distal part, at least  $t_1$  and  $t_3$  with dpr, no subcostal break,  $r_1$  long, anal vein not reaching wing margin, axillaris weak. Runs also to 62a ..... sp.n. 54, Sciomyzidae
- 37 (36) Sternopleuron with only 1 bristle present near hind upper margin (I, fig. 72). Mid- and hind-tibia at centre without small bristles (I, fig. 76). 3 dc ..... *Prodryomyza electrica* HENNIG, Dryomyzidae
- 37a Mid-femur with 1 anteroventral bristle, 4 dc, 4<sup>th</sup> dc directly behind suture, 1 pp and additional hairs, anal cell with very small point, 2<sup>nd</sup> antennal segment long, 34 pseudotracheae, epandrium huge, aedeagus coiled at tip ..... sp.n. 55, ?Dryomyzidae
- 38 (27) First radial vein ( $r_1$ ) completely bare.
- 38a Underneath of  $f_1$  with a row of short bristles,  $f_2$  and  $f_3$  bare,  $r_{4+5}$  and  $m_{1+2}$  convergent, at wing edge close together; 4 ors, prs, 2 dc (anterior short), ia, at least  $t_2$  and  $t_3$  without dpr, sc complete, subcostal break, wing 3.95 mm ..... sp.n. 56
- 39 (48) Mesopleuron at hind margin with 1 or more long and strong bristles (I, fig. 144, 186, 230, 256; II, fig. 20). Attention, short bristles: compare couples 40 (II, fig. 24), 84 (I, fig. 116). Prescutellar bristles (prsc) present (I, fig. 248).
- 40 (41) Each side with only 1 fronto-orbital bristle present (II, fig. 19) ..... *Glaesolonchaea electrica* HENNIG, Pallopteridae
- 40a 2 ors and 6 reclinate orbital setulae on dark orbits, long sclerotized dark subcostal cell (between sc and  $r_1$ ); pvt parallel, prs, 1-5 small m (number and length variable), 1-2 st, prsc, 8-9 acr-rows, at least  $t_1$  and  $t_2$  with praecapitals, 6<sup>th</sup> tergite and huge epandrium articulated bent down, long acute surstyli, lasso-formed aedeagus, males with long pleural appendix between 5<sup>th</sup> tergite and sternite, wing 2.18 mm ..... sp.n. 57, ?Chamaemyiidae
- 40b Costa break with strong bristle, costa bristled between break and humeral crossvein like extant Carnidae; vi, 2 ors, oc upright-divergent, prs, 2 m, 2 st, 2 dc, 0 prsc, 0 ia,  $f_1$  with 6 ventral,  $f_2$  with 4 anteroventral bristles, all t with dpr, wing 2.19 mm ..... sp.n. 58
- 40c Arista pectinate with dorsal and ventral rays, 0 vi, 2 ors, oc long divergent, pvt parallel, prs, 2 pp, 1 m, 2 st, 3 dc, 0 prsc, at least  $t_1$  and  $t_3$  with dpr,  $f_2$  with 8 and  $f_3$  with 12 anteroventral bristles,  $t_2$  with at least 5 posterolateral bristles, 3<sup>rd</sup> antennal segment densely pubescent, body 3.62 mm ..... sp.n. 59
- 40d Head broader than thorax, eyes large, weak vi present 2 ors, 1 st; oc long, a small ocellar triangle present, pvt parallel, 0 pp, 2 dc, prsc, 4 arc-rows, all t without dpr, very small costal spinules present, subcostal cell narrow, body/wing both 2.24 mm ..... sp.n. 60
- 40e 0 vi, number of ors ?, 1 pp, 1 m, mesopleuron without hairs, 0? st, 2 dc, prsc,  $f_1$  with 6 dorsal,  $f_2$  with 3 anterolateral,  $f_3$  with 2 posterolateral bristles, many short costal spinules, sc curves up to costa in an angle of 100°, round surstyli separated from epandrium, wing 3.02 mm ..... sp.n. 61
- 40f Arista with long dorsal and ventral rays, 2 sa (the anterior near suture may be called praearalar); 2 ors, oc long, pvt divergent, 0 prs, 1 pp and 5 small setulae nearby, 2 m, 2 st, 2 long and 1 short dc, prsc weak, 2 small la, at least  $t_1$  and  $t_2$  without dpr, costa without break, abdomen lateral behind halter with group of bristles, body 5.3 mm ..... sp. n. 62
- 40g Complicated spoon-like appendices on epandrium, 0 m but many short bristles on mesopleuron, lunula flat; 1 or 2 (?) ors, oc divergent, pvt parallel-divergent, 1 pp, 2 st, 2 dc, long prsc, at least  $t_2$  and  $t_3$  with dpr, subcostal cell sclerotized, dark, body 2.13 mm ..... sp.n. 63
- 40h Body/wing 2.39/2.28 mm, 4-5 rows of acr, 3<sup>rd</sup> antennal segment small, anal cell rudimentary; 0 vi, 2 ors, oc proclinate, pvt parallel-divergent, short, 1 m, 1 st, 2 dc, prsc, ventral side of  $f_1$  distally with 1-2 strong bristles,  $f_2$  and  $f_3$  bare, at least  $t_2$  without dpr ..... sp.n. 64



**Fig. 15:** Milichiidae, *Phyllomyza* sp., ♂, body 1.8 mm, lateral habitus; det. I. Brake; coll. HOFFEINS 878-3.



**Fig. 18:** Pyrgotidae, undescribed species, ♂, body 4.1 mm, lateral habitus; coll. HOFFEINS 1284-2.



16



17

**Fig. 16-17:** Pyrgotidae, undescribed species, ♂, body 4.1 mm; lateral habitus and details of left mid tibia with extended tibial spur. Specimen from autoclaved amber, frontal part with important characters of head partly obscured by translucent resin layers; coll. HOFFEINS 1284-1.



**Fig. 19:** Chloropidae, *Protoscinella electrica* HENNIG, ♀, body 2.5 mm, length of mesonotum 0.8 mm, mesonotum and scutellum in dorsal view showing the typical three central impressed grooves with "criss-cross"-arranged acrostichal setulae and short macrochaetae; compare chapter variability; coll. HOFFEINS 964-2.

- 41 (40) Each side 3 or more fronto-orbitals present (II, fig. 19).
- 42 (43) Presutural bristle absent or a weak one present (I, fig. 185). Postvertical bristles divergent (I, fig. 182, 183). Vibrissae present, 3 pairs of scutellar bristles, posterior crossvein shorter than end-section of  $m_{3+4}$ , 2<sup>nd</sup> antennal segment with triangular projection at outer surface . . . . .
- ..... *Electroclusiodes meunieri* (HENDEL), Clusiidae
- 42a 3<sup>rd</sup> antennal segment very small and slightly sunken in 2<sup>nd</sup> article, higher than long, arista terminal, anal cell rudimentary, prs inserts very low; 0 vi, 4 ors, oc proclinate, pvt divergent, 0 m, 2 dc prsc, ipa probably absent, 4 rows of acr., all t with dpr, genae bent under, wing 2.15 mm . . . . . sp.n. 65, ?Clusiidae
- 42b Anterior and longest one of 4 ors bent inwards, 2<sup>nd</sup> antennal segment with triangular extensionis at outer surface, prsc small or missing. Species is similar to *E. meunieri* . . . . .
- ..... sp.n. 66, *Electroclusiodes* sp., Clusiidae
- 42c Anterior one or two of 3 ors bent inwards, posterior one bent back- and outwards, pvt absent, costa ends at  $r_{4+5}$ ,  $r_{2+3}$  and  $r_{4+5}$  strongly convergent towards end, nearly touching, posterior cross vein absent; oc upright, 0 prs, 1 pp, 1 m, 1 st, 2 dc 0 prsc, ipa absent, 4-5 rows of acr, ap widely separated,  $f_1$  with 1 bristle in basal ventral position, body and wing 1.99 mm (Baltic and Bitterfeld amber) . . . . . sp.n. 67, ?Carnidae
- 42d Try also couplet 43a with very peculiar characters but unknown pvt-character.
- 42e Outside of 2<sup>nd</sup> antennal segment with triangular projection at outer surface, clypeus prominent, 4 ors, 3 pp, 3 pairs of scutellars (one on the disc); vi, 2 prolonged if above lunule, pvt divergent, 2 d, 2 m (lower short), 1-2 st, prsc, 10 rows of acr, all f bare, all t without dpr, subcostal break, body/wing 3.56-4.15/2.96-3.41 mm . . . . . sp.n. 68, *Electroclusiodes*, Clusiidae
- 42f Length of 3<sup>rd</sup> antennal segment nearly 2-times its height, subcosta complete, bent towards subcostal break in an angle of 100°, subcostal cell large, pvt parallel, 6-7 ors, oc short, 3 pp, 2 sa (the anterior also called praearal); vi, prs weak or absent and near notopleuron, ia, 2 la, all t with dpr, wing 4.88 mm. If m is judged to be short (couplet 39), then go to couplet 79 . . . . . sp.n. 69, ?Sciomyzidae
- 42g Head round, 2<sup>nd</sup> antennal segment with triangular projection at outer surface, legs relatively long; 3 ors, pvt divergent, 0 prs, 4 dc, prsc, 3.8 mm . . . . . sp.n. 70
- 42h 4 ors, posterior crossvein stands far basally on  $m_{3+4}$ ; vi, 0 prsc, 2 dc . . . . . sp.n. 71
- 42i Small species, ap long and widely separated, genae below eyes narrow, small spinulae along costa; vi, pvt convergent, 1 st, 3 dc, prsc, no prominent bristle on  $f_1$  . . . . . sp.n. 72
- 42k Short costal spinules in even distances,  $r_1$  long ending near mid of wing,  $r_{4+5}$  conspicuously bent backwards, at its end parallel with  $m_{1+2}$ ; vi, 3 ors, pvt divergent, 0 prs, 1 long pp, 1 m, 2 st, 2 dc, prsc, at least  $t_1$  without dpr, body/wing 3.56/3.12 mm . . . . . sp.n. 73, ?Heleomyzidae
- 42l Body/wing 2.28/2.35 mm, occiput (back of head) concave, eye covers whole head side, vi and h absent; 3 weak ors, weak proclinate oc, pvt weak, upright-proclinate, tiny pp, 1 m, 1 st, 2 dc, 0 prsc, 4 rows of acr, all f bare, all t without dpr, 1 spur at end of  $t_2$ , femora very slender, sc and  $r_1$  near together, jowl below eye linear, 3<sup>rd</sup> antennal segment slightly longer than high with prolonged pubescence . . . . . sp.n. 74
- 42m Body and wing both 2.78 mm, 3<sup>rd</sup> antennal segment relatively large, 3 long ors, 1 long pp, meso- and sternopleuron densely pilose; vi, oc long, pvt short, convergent-crossed, 2+1 small m, 1 st, 3 dc, (probably prsc),  $t_2$  with 1+3 terminal spurs . . . . . sp.n. 75
- 42n Ocelli close together, pvt divergent, long, sockets touching themselves, prs absent, small costal spinules in narrow distances, 4 scapular bristles in transverse row; vi strongly convergent, 3 ors, oc extremely long, central occiput with dense group of setulae, 1 m + 7 small bristles, 2-3 dc, scutellum large, prsc, at least  $t_1$  and  $t_3$  with dpr,  $t_1$  with cleaning comb,  $t_2$  with spur at end,  $mt_3$  with cleaning brush basally, body/wing 4.78/3.90 mm . . . . . sp.n. 76
- 42o 5-6 ors, the 2 or 3 anterior ones bent inwards,  $r_1$  ends near mid of wing, pvt upright- divergent; oc small, 4 small reclinated m, 4 st, 5 dc (the 2 anterior ones very small), ap relatively near together, jowl below eye bent under, 3<sup>rd</sup> antennal segment round, black, body/wing 2.68/2.39 mm . . . . . sp.n. 77
- 43 (42) Presutural bristle present (prs; I, fig. 142, 231, 256). Postvertical bristles (pvt) convergent (I, fig. 139, 140, 228, 254).
- 43a (The pvt are not visible, probably they are absent). One ocellus only, claws very short and not evenly curved but bent over in an abrupt angle of 90°, parallel and closely approximated, pulvilli braced sideways (see text); ors long and weak, 7-8 ors: 3 posterior reclinate and 4 (one side 5) anterior (inserted anteriorly of ocellar triangle) inclinate, oc short and divergent, pp not detectable, if present then they are very

- short, 1 st,  $t_3$  with dpr,  $t_2$  with very long apical spur and one shorter spur, subcostal break, short 2<sup>nd</sup> antennal segment (!), mid coxal prong absent, body 4.1 mm ..... sp.n. 78, Pyrgotidae
- 43b Four reclinate ors, 3 lower inclined ori, 2 pairs of long if, 4 st, 2m, face with antennal pits, epandrium round with large-scaled surstyli and gonites ..... sp.n. 79
- 43c Three reclinate ors, antennae in deep foveae, behind vti a further convergent bristle, vi bent inwards, 0 st, oviscape. Compare couplet 56a ..... sp.n. 80, *Meoneurites* sp., Carnidae
- 44 (45) Sternopleuron with 3 long and strong sternopleural bristles along upper margin (I, fig. 144). Each side 4 fronto-orbitals (ors), the anterior one is bent inwards (I, fig. 139, 140). Vibrissae absent (I, fig 138). Intra-alar bristle (ia) present (I, fig. 142) ..... *Hemilauxania incurviseta* HENNIG, Lauxaniidae
- 44 a 6 ors, 1 ia, 2 sa (= 1 sa + 1 praearal), 2 la. Go to couplet 42f.
- 45 (44) Sternopleuron with only 1 or 2 long and strong sternopleural bristles (I, fig. 230, 256). Each side only 3 ors (I, fig. 227, 228, 254, 255). The ia bristle absent. Vibrissae present (I, fig. 227, 229, 255).
- 45a 2 st, 4-5 ors (the anterior one probably inclinate), 2 h, axillaris ( $a_2$ ) distinct but not reaching wing margin; pvt convergent, 2 m, 3 dc (the 2<sup>nd</sup> and 3<sup>rd</sup> small and near to the 1<sup>st</sup>), prsc, no bristle or spine on lower side of  $f_1$ , 1 small dorsal bristle on  $f_2$ , at least  $t_1$  and  $t_2$  without dpr, subcostal cell weakly dark sclerotized, epandrium with about 4 strong upright dorsal bristles ..... sp.n. 81
- 45b 6 ors, at least the 2 hind ocelli present (anterior one invisible),  $t_2$  without apical spur ..... sp.n. 82, Pyrgotidae
- 45c Go back to couplet 43a.
- 46(47) Anterior fronto-orbital bristle bent inwards (I, fig. 228). 1<sup>st</sup> femur without a ventral spine ..... *Gephyromyiella electrica* HENNIG, ?Chyromyidae
- 47(46) Anterior fronto-orbital bent backwards like the further ones (I, fig 254, 255). 1<sup>st</sup> femur with a ventral spine (I, fig. 257), a specimen in the coll. HOFFEINS with thinner and more basal spine ..... *Proanthomyza collaris* HENNIG, Anthomyzidae
- 47a As 47 but 1<sup>st</sup> femur without ventral spine, arista bare; mesonotum humped, clypeus prominent, sc ends near  $r_1$ ,  $t_1$  cleaning-comb absent; 3 m ..... sp.n. 83
- 47b 1<sup>st</sup> femur with ventral spine, mesonotum normal,  $t_1$  with apical cleaning comb, sc ends distinctly separate from  $r_1$  ..... sp.n. 84
- 47c Clypeus normal,  $t_1$  without and  $t_3$  with a cleaning comb, ap wide apart; vi small, oc long, pvt short and crossed-proclinate; 1 pp, mesopleuron with long hairs, 2-3 m, 1 st, 4 dc, prsc long,  $f_1$  with 5 dorsal and 10 ventral bristles,  $f_2$  with 2 anterolateral bristles, subcostal cell darkened-sclerotized, sc thickened at end, ends near  $r_1$ , genae below eye linear, body/wing 3.27/2.98 mm ..... sp.n. 85
- 48 (39) Mesopleuron without prolonged strong bristles at hind margin. Moreover the mesopleuron is bare or (rarely) finely haired (but compare 49 and 84: very finely haired).
- 48a Large species (body estimated 6.2 mm), costa with spinules, subcostal cell dark; h, 2 n, prs, 1 pp, 0 m, 1 st, 3-4 dc (4<sup>th</sup> small), prsc, ap longer than la (compare couplet 14),  $f_1$  with 1 anterolateral and 4 long and further weak ventral bristles, all t with dpr, strong femora, long  $r_1$  ..... sp.n. 86, ?*Proneottiophilum*, Proneottiophilidae
- 48b Scutellum flat above (not convex), 1 dc and prsc tiny ..... sp.n. 87
- 49 (50) Each side only 1 fronto-orbital bristle present (II, fig. 10). Vibrissae absent, h and prsc present, size variable, wing 1.76-3.66 mm ..... *Morgea mcalpinei* HENNIG, Pallopteridae
- 49a Spinules along costa, pp and h and prsc absent, sc ends far from  $r_1$ ; vi, 1 ors, pvt long and parallel, prs, 0 m, 1 st, 2 dc,  $f_2$  anteriorly with 1 bristle in distal third, all t with dpr, genae as broad as 3<sup>rd</sup> antennal segment high, body/wing 4.68/5.51 mm. Similar to couplet 49h ..... sp.n. 88, ?Sciomyzidae
- 49b 3<sup>rd</sup> antennal segment distinctly longer than high, vi and ors and oc absent, pvt convergent and widely apart, 1 short dc very near to scutellum. Go to couplet 61.
- 49c Pectinate arista (rays on both sides), many strong peristomal bristles, 2<sup>nd</sup> antennal segment cap-like, clypeus prominent, proboscis large, prsc absent ..... sp.n. 89, Periscelididae
- 49d Clypeus very prominent, costal spinules, h absent; vi, 1 ors and 8 reclinate orbital setulae, oc long, pvt parallel, 0 m, 1 st, 2 dc, 0 prsc,  $f_2$  with 1 strong anteroventral bristle, all t with dpr, subcostal break, axillaris present, jowl bent under the eye, as broad as 3<sup>rd</sup> antennal segment, wing 3.56-4.88 mm ..... sp.n. 90, ?Sciomyzidae
- 49e Clypeus prominent, costal spinules absent, h and prs present; 0 vi, 1 ors, oc long, pvt long divergent, prs, 1 pp, 0 m, 2 st, 2 dc, 0 prsc,  $f_1$  with 7 dorsal and 3 strong/9 weak ventral bristles,  $f_2$  bare,  $f_3$  distally ventral

- with 2 strong bristles, subcostal cell dark sclerotized, subcostal break, genae narrow, equal with diameter of  $t_1$ , oviscape, epandrium with acute projection, wing 3.90-4.00 mm ..... sp.n. 91, *Morgea* sp., Pallopteridae
- 49f Clypeus prominent, costal spinules absent, h present, prs absent; vi tiny, 1 long ors, long oc, short divergent pvt, pp probably absent, 0 m, 1 st, 2 dc 0 prsc, all f seem to be bare,  $t_1$  with dpr and terminal cleaning comb, 3<sup>rd</sup> antennal segment small, wing 3.12 mm ..... sp.n. 92
- 49g Clypeus very prominent, bent upwards, costal spinules short, close together, separated by normal setulae, 1 h and 2 st present; vi very long and thin basally, oc long and upright-parallel, pvt convergent, 0 pp, 0 m, 2 st, 2 dc, 0 prsc, sockets of ap wide apart,  $f_1$  with 2 dorsal bristles (one basal and one distal),  $f_2$  with 1 long anterolateral bristle in distal half,  $t_2$  with and  $t_3$  without dpr,  $r_1$  short,  $r_{2+3}$  long, a small sclerotized plate below female cerci, wing 3.27 mm ..... sp.n. 93
- 49h Costal spinules present, 0 h, 1 st, prs, 0 prsc; vi, 1 or, oc long, setulae on mesopleuron, 1 st, 2 dc, 6 rows of acr, jowl bent under the eye, 3<sup>rd</sup> antennal segment small, wing 4.00 mm. Similar to couplet 49a, genae narrower ..... sp.n. 94, ?Sciomyzidae or ?Heleomyzidae
- 49i Tiny species, body/wing 1.79/1.71 mm, face convex (artificially?), the following bristles are absent: pvt, vti, prs, pp, m, st, ia, epa, ipa, sa, prsc, head broader than thorax, 3<sup>rd</sup> antennal segment very short, arista inserted basally, very long and thin; vi, 1 long ors in front of which is a row of 3 meticulous setulae, oc long proclinate, vte, all four bristles 1 h and 1+1 n and 1 h very short, mesopleuron without hairs, sternopleuron with 5 fine hairs, 1 dc, only 2 rows of acr consisting of 4 setulae each, ap upright, all f bare, all t without dpr,  $t_1$  with cleaning comb, long bristle at end of  $t_2$ ,  $r_1$  long,  $r_{2+3}$  short ending nearer to  $r_1$  than to  $r_{4+5}$ , sc bent steeply to costa, costa-break absent, genae linear in front, very broad at rear, huge looped aedeagus with dense long setulae ..... sp.n. 95, ?Aulacigastridae or ?Periscelididae
- 50 (49) Each side at least with 2 fronto-orbitals (attention: couplets 60 and 61 of HENNIG includes text and one species without ors).
- 51 (60) One or more fronto-orbitals bent inwards (I, fig. 238, 245, 246, 273; II fig 35, 46).
- 52 (53) Postvertical bristles convergent (II, fig. 35, 36) or at least parallel [key of HENNIG 1971].
- 52a(52b) Each side 3 upper fronto-orbitals present, all bent outwards (over the edge of eye) ..... [the valid taxon:] *Phyllomyza jaegeri* HENNIG, Milichiidae
- 52b(52a) Each side only 2 fronto-orbitals present, which are bent outwards, as well 2 anterior ors bent inwards ..... *Pseudodesmometopa succineum* HENNIG, Milichiidae
- 52c Upper 2 ors bent upwards and outwards (or the anterior only outwards), lower 2 ors bent inwards, proboscis strongly elongate and acute, palpi long and thick; vi, 2 rows of reclinate interfrontals, the anterior pair proclinate, small divergent oc, small widely separated convergent pvt, 1 pp, 0 m, 1 st, 2 dc, prsc, 8 rows of acr,  $f_1$  with 2 dorsal setae, a ventral spine, and 10 posteroventral bristles in row,  $f_2$  bare, all t with dpr, costa ends at  $m_{1+2}$ , sc as a fold towards costa-break near  $r_1$ , anal cell rudimentary, analis absent, axillaris present, face concave with keel between 1<sup>st</sup> antennal segments, 3<sup>rd</sup> antennal segment ball-like, body/wing 1.66-2.08/1.22-1.76 mm ..... sp.n. 96, *Pseudodesmometopa* sp., Milichiidae
- 52d Upper 3 ors bent backwards, one anterior ors (widely separated from the upper) bent inwards, proboscis strongly elongate, palpi short; vi, if on yellow frons all proclinate, a pair of convergent anterior ones long, 2/3<sup>rd</sup> of their length crossing the lunule, oc long, pvt parallel, vertex with 4 small inclined bristles behind pvt till pvt, 0 pp, 0 m, 2 dc, 2 st, sternopleuron haired, prsc, ipa absent, 10 rows of acr,  $f_1$  posterodorsal with 8 bristles,  $f_3$  with 1 long posterodorsal bristle in distal third,  $r_1$  relatively long, subcostal cell light and narrow, alula present, face with deep foveae and broad keel, 3<sup>rd</sup> antennal segment slightly higher than long, together with 1<sup>st</sup> and 2<sup>nd</sup> one yellow with prolonged upwards directed pubescence, body and bristles yellow except one dark n, body/wing 1.88/2.03 mm ..... sp.n. 97, Milichiidae
- 52e Two upper ors bent backwards and outwards, 1 lower inclinate ors, proboscis moderately elongate, label-lum with deep incisure, ending in two narrow tips with only 1 or 2 pseudotracheae each side, palpi not elongate, widened distally ..... sp.n. 98
- 53 (52) Postverticals (pvt) divergent or absent.
- 54 (55) Only 2 fronto-orbitals present, the anterior one bent inwards, the posterior backwards (I, fig. 238). Mouth edge protruding (I, fig. 240). (Hind edge of head peculiarly excavated. Postvertical bristles absent. Mesopleuron with fine hairs). Arista more or less bare, vte and vti present ..... *Protaulacigaster electrica* HENNIG, Aulacigastridae

- 54a Similar to preceding species, but arista pectinate with dorsal and ventral rays, pvt and vti absent, instead of them small proclinate bristles present; 2 n, prs and prsc absent, ap and la, costa without break, small species. (Species runs also to 5d) ..... sp.n. 99, ?Aulacigastriidae
- 54b Clypeus prominent, 2<sup>nd</sup> antennal segment cap-like, 5 ors, the 2 anterior ones inclinate, f<sub>1</sub> bristled on lower side; 2 dc ..... sp.n. 100, ?Aulacigastriidae
- 55 (54) Four fronto-orbitalis present. Mouth-edge not protruding, postverticals divergent (in *Anthoclusia* they are developed only as very fine hairs).
- 56 (57) Antennae embedded in deep foveae (I, fig. 274) [this character is supervalue]. Each side of scutellum with 3 bristles (I, fig. 278). Genae in front with only one long and strong vibrissa (I, fig. 275, 276). Compare couplets 42c, 42d. Female cerci fused [discussed by HENNIG, confirmed by M.v.T.] ..... Meoneurites enigmatica HENNIG, Carnidae
- 56a As couplet 56 but scutellum with 2 pairs of bristles only, both bent backwards, female cerci very narrow, if fused not visible. Compare couplet 43c ..... sp.n. 101, Meoneurites sp., Carnidae
- 57 (56) Antennae not embedded in foveae. Each side of scutellum with 1 or 2 bristles. Each side of genae in front with about 4 equally long and equally strong bristles (I, fig. 246). If only 2 equal bristles present go to couplet 59a.
- 57a Genae broad, eyes oval, 3 pairs of scutellar bristles, vi and 9 fine peristomal setae ..... sp.n. 102, Clusiidae
- 57b Each side of pvt a further convergent bristle, 3 pairs of scutellars, h, 2 n, prs, 2 dc, sc complete ..... sp.n. 103
- 58 (59) In the wing venation the distance between r<sub>2+3</sub> and r<sub>4+5</sub> is shorter than the distance between the ends of r<sub>4+5</sub> and m<sub>1+2</sub> (I, fig 250). Each side of scutellum with 1 lateral and 1 apical bristle (I, fig 248). Prescutellar bristles (prsc) present (I, fig 248). Species runs also to couplet 73, comment see there ..... Anthoclusia gephyrea HENNIG, Neurochaetidae
- 59 (58) In the wing venation the distance between r<sub>2+3</sub> and r<sub>4+5</sub> is about 1½ the length of the distance between the ends of r<sub>4+5</sub> and m<sub>1+2</sub> (III, fig. 31). Each side of scutellum with 1 (the apical) bristle only. Prescutellars (prsc) absent. 2 ors reclinate and 2 ors inclinate, 3<sup>rd</sup> antennal segment with long pubescence, vi + 3 peristomal bristles ..... Anthoclusia remotinervis HENNIG, Neurochaetidae
- 59a Similar to 59, but 3<sup>rd</sup> antennal segment and arista with short pubescence, vi and 1 peristomal bristle, ventral side of f<sub>1</sub> with 8 spinules and 6 bristles ..... sp.n. 104
- 59b Similar to 59, but 3<sup>rd</sup> antennal segment small, 3 reclinate and 1 inclinate ors, 0 prs, mesopleuron only hairy, 2 dc, t without dpr, 0 prsc, ap and only 1 small la ..... sp.n. 105
- 60 (51) All fronto-orbital bristles (if such present at all) bent backwards (recline).
- 61 (62) Vertical- and fronto-orbital bristles absent. Head only with one pair of small convergent bristles present behind ocellar triangle (I, fig. 267A; III, fig. 42). Arista very short, shorter than the elongate and downwards directed 3<sup>rd</sup> antennal segment (I fig. 266A). Compare couplet 49b ..... Phanerochaetum tuxeni HENNIG, Cryptochetidae
- 62 (61) Vertical bristles (at least 1 pair), fronto-orbital bristles (at least 2 pairs), and postvertical bristles all present. Arista of normal size: longer than the roundish or short-elliptic 3<sup>rd</sup> antennal segment.
- 62a Large fly, go back to couplet 36a.
- 63 (70) Neither humeral (h) nor presutural bristle (prs) present. Postvertical bristles (pvt) always divergent. [Disagreement with I, fig. 1, parallel/convergent, fig. according with specimens in the von TSCHIRNHAUS-collection, and also with couplet 68-69, parallel].
- 63a Go to couplet 70a.
- 64 (65) Each side only 2 fronto-orbital bristles present (III, fig. 37, 38), in front of them 5 very short orbital setulae in row. Postvertical bristles (pvt; III, fig. 37) very short and fine. Wing venation: subcostal vein not reaching the costa (III, fig. 33); vein r<sub>2+3</sub> short, ending half way between r<sub>1</sub> and r<sub>3+4</sub>. Small species (body-length about 2 mm) ..... Succinasteia carpenteri HENNIG, Asteiidae
- 64a Similar to preceding, r<sub>2+3</sub> ends very near to r<sub>1</sub>, 2 rows of acr ..... sp.n. 106, Astiosoma sp., Asteiidae
- 65 (64) Each side 3 or 4 fronto-orbital bristles present. Postvertical bristles long and strong. Subcostal vein always reaching the costa. Larger species (body length at least 5 mm).
- 66 (67) Costa at ending of sc with break (I, fig. 11). Short reclinate ocellar bristles present, as well each side 4 fronto-orbital bristles (ors) (I, fig. 7, 8), the most upper one far behind ..... Cypselosomatites succini [sic!, corrected printing error] HENNIG, Cypselosomatidae

- 67 (66) Costa without subcostal break (I, fig. 31, 32). Ocellar bristles (oc) absent or tiny upright ones present. Each side only 3 fronto-orbital bristles present (I, fig. 16-19, 31, 32).
- 68 (69) Back of the head extended to protuberances (I, fig. 31, 32). Outer vertical bristle (vte) absent (I, fig. 31). Scutellum with only 1 bristle each side (I, fig. 33, 34). Only 1 pair of dorso-central bristles present (dc; I, fig. 33, 34). Compare also couplet 75a: scapular bristle present . . . . .
- ..... *Electrobata myrmecia* HENNIG, Micropezidae
- 68a As above, but weak protuberances, 3-4 strong ors, small oc present, vte and vti, palpi probably very small; 3 upright h at inner edge of callus, 1+1 n, 3 st, 1 dc, epa and ipa, sa, 2 rows of weak acr, 0 la, erect ap, absent macrochaetae: prs, pp, m, prsc, ia, la, all femora bare, at least t<sub>1</sub> without dpr, body/wing 6.59/4.54 mm . . . . . sp.n. 107, *Electrobata* sp., Micropezidae
- 68b Head without protuberances, palpi with group of strong upright bristles, vte absent, antennae embedded in foveae, male with large appendix on last sternite; 2 ors, 1 dc, only 1 pair of scutellars . . . . . sp.n. 108, Micropezidae
- 68c Head with weak protuberances, palpi long and without prominent bristles, vte and vti present, outer tip of fore-coxa with acute sclerotized small protuberance; 3 weak ors, tiny oc, 0 prs, 2 tiny pp, 0 m, 1 dc, 0 prsc, 0 ipa, sa and acr absent, 0 la, erect ap, ♂ body/wing 8.38/5.71 mm . . . . . sp.n. 109, Micropezidae
- 69 (68) Back of the head without protuberant prolongations (I, fig. 16-19). Vte present (I, fig. 16-19). Each side of scutellum with 2 bristles (I, fig. 20-22). Mesonotum with 2 pairs of dc (I, fig. 20-22) . . . . . [forgotten in original:] *Electrobata tertaria* MEUNIER, Micropezidae
- 70 (63) At least the humeral bristle (h) present. Regard exceptions couplets 70a, 70 b.
- 70a Humeral (h) and prs present; vi, 2 ors, pvt convergent, 2 d, 1 anteroventral f<sub>2</sub>-bristle, costal break . . . . . sp.n. 110
- 70b Humeral (h) and probably prs present, prominent clypeus, fly pitch-black . . . . . sp.n. 111
- 71 (78) Presutural bristle (prs) absent (I, fig. 6, 148, 152; II, fig. 29).
- 72 (75) 4 pairs of fronto-orbital bristles present (ors; I, fig. 245, 246; II, fig. 26, 27).
- 72a Small dull ochrous species, 10 or more short and even ors along eye, the most posterior one near vti slightly stronger and longer. Thickened long yellow palpi peculiarly overtopping the mouth edge, proboscis neither narrow nor distinctly elongate, only 1 small erect sa, mesonotum with 3 rugose long central grooves and, each side, one shorter, broader and flatter lateral-posterior one, all these "filled" by criss-cross arranged microchetae, mesonotum with 5 black longitudinal stripes on yellow ground . . . . .
- ..... sp.n. 112, *Tricimba* LIOY, Chloropidae
- 72b Larger, body/wing 2.44/2.05 mm, sa and la absent (!); 2 vi each side (!) and 1 further long peristomal bristle, 3 ors, pvt parallel-convergent and widely separated, long h, 1 pp, 0 m, 0 ipa, 1 long and 2 short f<sub>1</sub>-bristles, 3 dorsal f<sub>3</sub>-bristles, genae broad, equal f<sub>1</sub>-diameter . . . . . sp.n. 113
- 72c 3 ors, 1 vi, pvt long, divergent, mesopleuron hairy, 1 m, f<sub>1</sub> bare, arista dorsal, wings dark . . . . . sp.n. 114
- 73 (74) Posterior crossvein (tp) longer than the last section of m<sub>3+4</sub> (I fig. 250). Arista pennate with long rays (I, fig. 247). Fore-femora with strong ventral spines (I, fig. 251). Species runs also to couplet 58 . . . . .
- ..... *Anthoclusia gephycra* HENNIG, Neurochaetidae
- 73a Crossvein tp much shorter, 3 pairs of scutellars, 2<sup>nd</sup> antennal segment with triangular extension at outer surface, arista terminal; 1 vi, pvt divergent . . . . . sp.n. 115, Clusiidae
- 74 (73) Posterior crossvein shorter than the last section of m<sub>3+4</sub> (II, fig. 30). Arista with short hairs (II, fig. 26, 27). Fore-femora without ventral spines, back of head strongly concave. In the description (II, 19-22) it is constated that ipa and a 3<sup>rd</sup> pair of sc are absent; in our inclusions both are present . . . . .
- ..... *Xenanthomyza larssonii* HENNIG, Clusiidae
- 74a As couplet 74 but 3<sup>rd</sup> antennal segment round, sa absent, mesonotum with 5 black stripes like many extant Chloropidae; vi, 4 ors, pvt very short, divergent, 0 m, 1 st, 2 dc, 0 prsc, 0 ipa, t<sub>1</sub> with, t<sub>3</sub> without dpr, body/wing 2.23/1.66 mm . . . . . sp.n. 116, Clusiidae
- 74b 3<sup>rd</sup> antennal segment very short with terminal reclinate arista, 2<sup>nd</sup> with family-typical outside extension towards 3<sup>rd</sup> body/wing, lower side of r<sub>1</sub> with 3 setulae, epandrium movable separated from tergite; vi, 4 ors, pvt divergent, 0 pp, 0 m, 0 st, 1 dc, prsc, 0 ipa, t<sub>2</sub> with end-spur, r<sub>1</sub> thickened at end, near sc, eyes shorter than high, body/wing 2.50/1.81 mm . . . . . sp.n. 117, Clusiidae
- 74c Last section of m<sub>3+4</sub> equals length of tp, 3<sup>rd</sup> antennal segment narrowed distally, longer than high, 2 rows of acr, la absent; frons, antennae and tip of scutellum yellow . . . . . sp.n. 118, ?Clusiidae
- 74d Back of head concave, arista short pennate, 2 rows of acr, clypeus and mesonotum brilliantly shining, 2.20 mm, 2 vi, 4 ors, oc long, pvt short crossed, (prs absent?), ?0 m, ?2 st, 3 dc, 0 prsc, 0 ipa, ap long and cur-

- ved, 9 ventral  $f_1$ -setae, all t without dpr, sc complete, ends at costa-break near  $r_1$ , wings long, equal to body length, 2.20 mm ..... sp.n. 119, ?Anthomyzidae
- 74e Four ors, pvt short and divergent, the short 3<sup>rd</sup> antennal segment embedded in the 2<sup>nd</sup> antennal segment, arista terminal; mesopleuron bare and without m, sa present, subcostal cell small, lower side of  $r_1$  without setulae, femora without ventral bristles ..... sp.n. 120, Clusiidae.
- 75 (72) Each side only 2 fronto-orbitals (ors).
- 75a Large species, 3 ors, the anterior one is small, vibrissae absent ..... sp.n. 121, Micropezidae
- 75b Small species, 3 ors, vi present; pvt convergent; 0 m, 2 st, 2dc, dpr absent in all t, sc ends as a fold near  $r_1$ ,  $f_1$  without a bristle ..... sp.n. 122
- 75c Small species, body/wing 2.50/2.20 mm, clypeus prominent, 3 ors in posterior half of frons, pvt small, divergent; vi inclinate, 2 weak h, 0 prs, 0 m, 2 st, 2 dc, prsc, 10 acr-rows,  $f_1$  with row of 7 weak ventral setae,  $f_3$  with 1 anterior distal bristle, mt3 with brush on lower side,  $r_1$  short, genae linear, complicated male genitalia ..... sp.n. 123
- 76 (77) Postvertical bristles (pvt) divergent or parallel (I, fig. 121-123). Sternopleuron bare and without sternopleural bristles (I, fig. 6). Each side of scutellum with 1 bristle only. No vibrissae present (I, fig. 121-123); [attention: compare I, fig. 121, showing a remnant of a strong bristle behind the deepest point of the eye (bristle present also in other specimens), this may be taken as a vi]. Large species: body length 8.5 mm ..... *Sepedonites baltica* HENNIG, Sciomyzidae
- 76a Vibrissae absent, pvt parallel, 0 prs, 1 st,  $r_1$  ends mid of wing; 2 strong ors, orbital setulae proclinate, 0 pp, 0 m, 2 dc, 0 prsc, 8 acr-rows, all t with dpr, subcostal cell dark, axillaris ( $a_2$ ) present, mid of face rised, genae below eyes slightly broader than  $t_1$ -diameter, thick black palpi and black antennae, female cerci 5 times longer than broad, body/wing 2.73/3.22 mm ..... sp.n. 124, Sciomyzidae
- 76b Vibrissae absent, pvt divergent,  $r_{4+5}$  and  $m_{1+2}$  slightly convergent, 2 short ors far behind; 2 st, 2 dc, prsc long, all t without dpr,  $t_1$  with cleaning comb, subcostal cell large and sclerotized and dark, no subcostal break, rudimentary point of anal cell present, body 3.8 mm ..... sp.n. 125
- 76c Pictured wings, pvt divergent, 1 st, ap, 1-2 la ..... sp.n. 126
- 76d Long orbital setulae present, vibrissae present, pvt divergent, 3 st ..... sp.n. 127
- 77 (76) Postvertical bristles convergent, very short, (I, fig. 150). Sternopleuron with 1 long and strong sternopleural bristle (I, fig. 148). Each side of scutellum with 2 pairs of bristles (I, fig. 152). Vibrissae present (I, fig. 151). Small species: body length 2.3 mm ..... *Procremifania electrica* HENNIG, Chamaemyiidae
- 77a Postverticals absent, oc tiny, ipa absent, 2<sup>nd</sup> article of long arista at its base three times thicker than distally ..... sp.n. 128, *Procremifania* sp.n., Chamaemyiidae
- 78 (71) Presutural bristle present. If more than 1 prs: go to couplet 79.
- 79 (86) Postvertical bristles (pvt) divergent or parallel. Vibrissae absent. Compare also 26a.
- 79a Vibrissae present, adjacent to the divergent pvt a further convergent bristle on each side, 1 pair of if, proboscis sclerotized, short labellum bearing rasping teeth, oc strong and upright, 4 ors; 0 pp, 0 m, 3 st + 2 smaller setae, 0 prsc, 0 ia, 3 pairs of scutellar bristles, the basal one weak, sc ends far from  $r_1$ , small species (body/wing 2.25/1.88 mm) ..... sp.n. 129
- 79b Postvertical bristles and vi absent, 2 ors, orbital setulae present, anterior ones pro-, posterior ones reclinate; prs, 1 st, 2 dc, prsc, short legs, all t without dpr, body 2.14 mm ..... sp.n. 130
- 79c Postverticals minute, probably divergent, moderately long costal spinules,  $r_1$  long, subcostal cell narrow and dark, ends in mid of wing; 0 vi, 2 ors, oc divergent, 0 m, 1 st, 2 dc, prsc, ap long and divergent,  $f_1$  ventral with 7 bristles in row,  $f_2$  and  $f_3$  seem bare, 2<sup>nd</sup> article of arista long, long narrow surstyli narrowed in an acute tip, body/wing 1.96/1.98 mm ..... sp.n. 131, ?Lauxaniidae
- 79d 3<sup>rd</sup> antennal segment ball-like with terminal arista, vte absent, pvt parallel and bent forwards, 2 posterior dc, in front of these 7+5 long acr in row, 2+3 n (rare!), 3+3 pp on each side, halteres of sausage-form (artificial?), costa with spinules, lower calypter (at base of wings) with 4 spines along edge; vi, long oc, h, 1 m, 1 st, long prsc. (Species runs also to 19e as judgement if presence of presutural dc is difficult) .. sp.n. 132
- 79e Vibrissae present, 4 ors, 0 + 6 dc, 3 pairs of scutellar bristles ..... sp.n. 133
- 79f Strong vi and 7 peristomal bristles in 1 row present, 4 strong ors, 1 pair of convergent strong if above lunule, strong upright or proclinate oc, divergent weak pvt, 3<sup>rd</sup> antennal segment much shorter than high with a dorsal densely pubescent and strongly bent backwards arista; 1 tiny pp, 0 m, 1-2 st, 3 dc, prsc, 1 ia,  $f_1$  with 7 bristles above and many below in row,  $f_2$  and  $f_3$  bare, at least  $t_2$  and  $t_3$  with dpr, sc complete, ending near  $r_1$  and subcostal break, genae narrow, long narrow haired surstyli pointing down, 2<sup>nd</sup> antennal

- segment with triangular extension at outer surface, end-third of wing naturally smoky, body/wing 4.15/3.84 mm ..... sp.n. 134, Clusiidae
- 79g** Vibrissae absent, pvt parallel, 2 exceptional long bristles at hind corner of genae and no further strong peristomal bristles (unique among all seen species); pp long, dc, prsc, ap, 1 la, f<sub>2</sub> with 5 small anteroventral bristles, no subcostal break, no costal spinules, subcostal cell brownish, 6<sup>th</sup> tergite of male (in front of the epandrium) with a group of 14 dorsal erect bristles ..... sp.n. 135
- 79h** 3<sup>rd</sup> antennal segment very small, vi present, 2 ors, pvt divergent, 0 m, (probably 0 or at most 1 st), 2 dc with 3 further tiny ones till suture, 0 prsc, ap, 1 la, sc ends as fold near r<sub>1</sub>, tp far apical near wing margin ..... sp.n. 136
- 79i** If convergent pvt are small and genae below eyes are completely absent go also to 88 g (direction of pvt unclear).
- 80 (81)** Anal cell with angled posterodistal projection (I, fig. 98, 101). Different from HENNIG-description several specimens only with 1 h present, the longer one; pp very small, f<sub>1</sub> with 8-10 dorsal bristles, f<sub>2</sub> with 0-1(small) anteroventral bristle, f<sub>3</sub> with 2 anterodorsal bristles in apical half, t<sub>1</sub> with cleaning comb, mid of t<sub>3</sub> with 1-5 anterodorsal bristles, large round epandrium, body 6-8 mm ..... *Prosalticella succini* HENNIG, Sciomyzidae
- 80a** Similar to the preceding species, but 3<sup>rd</sup> antennal segment much smaller, round; oc upright, pvt short and parallel, vte, vti, 2 ors, lower one shorter and weaker, 0 vi, 1 h, 2 n, 1 prs, 1 pp, 0 m, 0 st, 2 dc, epa, ipa, sa, scutellum bare, la and ap both upright, f<sub>1</sub> with dorsal and ventral rows of bristles, all t without dpr, costa without break, costal spinules seem to be absent, sc and r<sub>1</sub> ending far from r<sub>1</sub>, r<sub>1</sub> bare, anal cell with tiny angled lobe at posterior corner, analis and axillaris ending both at wing edge, palpi narrow and strongly bristled, 2<sup>nd</sup> antennal segment without dorsal bristle, body 6.1 mm. [This and further species presently under study by L. KNUTSON] ..... sp.n. 137, Sciomyzidae
- 81 (80)** Anal cell without a corner (= an angled posterodistal projection).
- 82 (83)** Prescutellar bristles (prsc) absent ..... *Palaeoheteromyza investiganda* HENNIG, Sciomyzidae
- 82a** Prescutellars tiny, they may be partly absent. Go to couplet 87b.
- 82b** All acr absent, mesonotum shining but sparsely pubescent, la absent; vi absent, 3 ors, parallel upright oc, short divergent pvt, 1 dc with a row of at least 10 small setulae in front of dc, 0 prsc, very small sa near wing, all t without dpr, t<sub>2</sub> with apical short spur, r<sub>1</sub> short, ends near complete sc, r<sub>2+3</sub> very long and concave at rear, anal cell present, face with deep antennal-foveae, smallest amber acalyptate fly: body/wing 1.3/1.47 mm ..... sp.n. 138
- 83 (82)** Prescutellar bristles (prsc) present (I, fig. 117).
- 84 (85)** Mesopleuron is setulose (I, fig. 116). Distal parts of r<sub>4+5</sub> and m<sub>1+2</sub> parallel or slightly convergent (I, fig. 118). Attention: contradicting couplet 48, "or (rarely) finely haired" ..... "*Palaeoheteromyza*" *curticornis* HENNIG, Sciomyzidae
- 84a** Large species, arista with long dorsal rays, f<sub>2</sub> and f<sub>3</sub> thickened, f<sub>2</sub> with ventral spines, r<sub>4+5</sub> and m<sub>1+2</sub> not convergent ..... sp.n. 139
- 85 (84)** Mesopleuron is bare. Distal part of r<sub>4+5</sub> and m<sub>1+2</sub> strongly convergent ..... *Palaeotimia lhoesti* MEUNIER, Dryomyzidae
- 85a** Wing only 1.76 mm, pvt proclinate, subcostal cell dark. Go to couplet 87b.
- 85b** Mesopleuron bare, distal part of r<sub>4+5</sub> and m<sub>1+2</sub> only very slightly convergent, 1+5 pp, 4-5 dc, 4-5 st, ♂ body/wing 3.80/3.22 mm ..... sp.n. 140, Sciomyzidae
- 86 (79)** Postvertical bristles (pvt) convergent, (if tiny and parallel go to 87b).
- 87 (88)** Vibrissae are absent (I, fig. 127-130). Wing without a subcostal break (I, fig. 133, 134). Sternopleuron at upper margin with 4-5 long bristles (I, fig. 131). Anal vein very short (I, fig. 133, 134). 2<sup>nd</sup> antennal article also at inner side with a corner onto the 3<sup>rd</sup>, pp longer than in HENNIG's figure, also 4 dc occur, long female cerci, wing 2.83-3.12 mm ..... *Chamaelauxania succini* HENNIG, Lauxaniidae
- 87a** Only 1 st, mesonotum with 5 longitudinal black stripes on light ground (like many extant Chloropidae); 2 dc, prsc, ap, la, r<sub>3+4</sub> long ..... sp.n. 141
- 87b** Only 1 st, pvt tiny and proclinate, subcostal cell narrow, sclerotized and dark; 0 vi, 2 ors, 2 tiny pp, 0 m, 1 st, 1-2 dc, prsc both, absent and present, 6 acr-rows, all t without dpr, metatarsi very short, tarsi 2-5 and legs short, too, r<sub>4+5</sub> long, concave at rear, ovipositor seems slightly sclerotized at end, surstyli acute and short, a densely pubescent species, body/wing 1.52-1.96/1.54-1.79 mm. Runs also to couplet 85a ..... sp.n. 142

- 87c Moderately large clypeus protruding, short costal spinulae,  $r_{3+4}$  at rear strongly concave, parallel to  $m_{1+2}$ , divergent with  $r_{2+3}$ ; 2 ors, pvt parallel reclinate, 0 pp, mesopleuron without hairs, 1 m, 2 st, 2 widely separated dc, prsc, 4-acr rows, ap crossed and much longer than la,  $f_1$  distally with 2 ventral and 2 dorsal bristles,  $t_1$  without,  $t_2$  and  $t_3$  with dpr, femora slender, subcostal cell narrow, distally widened, no subcostal break, analis shortened, genae narrower than  $t_1$ , narrowest at rear, 3<sup>rd</sup> antennal segment with pubescence longer than diameter of basis of arista, female cerci long, body/wing 1.88/2.08 mm ..... sp.n. 143
- 87d Ocellar bristles long, parallel and reclinate, 2 ors, anterior reclinate orbital setulae present; pp long, 0 m, 1 st, 2 long dc, prsc,  $t_3$  with terminal spine and cleaning comb, subcostal cell small, axillaris developed, 3<sup>nd</sup> antennal segment on inner side with small prolongation on to the 3<sup>rd</sup>, wing 3.48 mm ..... sp.n. 144
- 88 (87) Vibrissae are present (I, fig. 205, 206, 211, 212, 218). Wing with a subcostal break at end of sc (I, fig. 207, 225). Sternopleuron at upper margin with at most 3 long sternopleural bristles. Anal vein reaching wing margin (I, fig. 207, 225).
- 88a No subcostal break, 2 ors, long oc, small pvt, 1 pp, 0 m, 1 st, 2 long dc, prsc, scutellum shiny and relatively flat, no costal spinules, sc ends far from  $r_1$ , all t with dpr,  $t_3$  with terminal spine, body/wing 3.02/2.93 mm ..... sp.n. 145
- 88b Anal vein not reaching wing margin, pvt short, 2 pp, 2 st, 0 prsc, sc complete, genae narrow, small species ..... sp.n. 146
- 88c Anal vein not reaching wing margin, pvt short, sc fading away distally, (pp seems to be absent); long proclinate oc, 3 long ors, 0 m, 2 st, 2-3 dc (the anterior short), 0 prsc, ipa absent, ap widely separated, axillaris absent, 3<sup>rd</sup> antennal segment with long pubescence, genae linear, eyes large, epandrium with a pair of strong distant dorsal bristles, with very thick ball-like male cerci, and acute and curved appendix, body/wing 2.03/2.08 mm ..... sp.n. 147
- 88d Weak costal spinules,  $r_{2+3}$  at tip bent upwards to costa,  $r_{4+5}$  and  $m_{1+2}$  slightly convergent, ipa absent; mesopleuron without hairs, 0 m, 2 st, 2 dc, 0 prsc, 4 acr-rows,  $f_1$  with 4 dorsal bristles,  $f_2$  and  $f_3$  bare, at least  $t_3$  without dpr and a terminal cleaning comb, analis long, axillaris absent, epandrium large, round, with a pair of upright dorsal bristles, small species ..... sp.n. 148
- 88e Anal vein reaching wing margin, large protruding clypeus, no costal spinules; 2 long ors, long oc, pvt small and crossed, 2 tiny pp, 0 m, 2 st + some hairs, 2 dc, 0 prsc, 6 acr-rows, last third of  $f_1$  with 1-2 dorsal bristles,  $f_2$  with 1 antero-ventro-lateral strong bristle, at least  $t_2$  with dpr and a terminal short spine, robust femora, subcostal cell brownish sclerotized, subcostal break, wing 3.12–3.56 mm ..... sp.n. 149, ?Heleomyzidae
- 88f Short costal spinules present and at close quarters, large 3<sup>rd</sup> antennal segment with long pubescence, width of genae below eyes equals the length of the 3<sup>rd</sup> antennal segment; long vi, 2 ors, long oc, crossed pvt, back of head strongly convex, 2 tiny pp, 0 m, no hairs on mesopleuron, 2 st + 1 small one, 2 dc, 0 prsc, slender femora, sc ends near  $r_1$  as a fold, face slightly concave, body 2.68 mm ..... sp.n. 150
- 88g Genae below the eyes completely absent, 2 vi of equal size, 2 ors and small reclinate orbital setulae, 14 acr-rows,  $r_1$  ends outwards of the middle of wing; short pvt probably convergent (species included also in couplet 79i), 1 long pp, 0 m, 4 long st, sternopleuron haired, 2 dc, prsc, all t with dpr,  $t_2$  with 2 spines and shorter spinules at ventral side, sc complete, surstyli long, acute and needle like, postabdomen movable, last tergite/pseudotergite prickly bristled, body/wing 3.27/2.68 mm ..... sp.n. 151
- 88h A subcostal break outwards of the humeral crossvein seems to be present; vi probably present, 2 ors, divergent oc, 0 pp, 0 m, mesopleuron bare, 1 st, 2 dc, prsc, 6 acr-rows, ap widely separated,  $f_1$  with about 5 dorsal bristles, axillaris present, genae below eyes equal about height of 3<sup>rd</sup> antennal segment, body 2.03 mm ..... sp.n. 152
- 88i Vibrissae long, peristomal bristles absent, narrow pubescent clypeus protruding, above the 1<sup>st</sup> antennal segment (scapus) a narrow transverse sclerite, adjacent ptilinal fissure very low, 0 pp, dense long pubescence around posterior spiracle; 2 ors (anterior short), oc very long, mesopleuron without hairs, 0 m, 2 st, 2 dc widely separated from front to rear just as the ap, 8 acr-rows,  $f_1$  with 1 distal dorsal, 1 distal anteroventral and 1 basal dorsal bristle,  $f_2$  with one anteroventral and  $f_3$  without a bristle,  $t_1$  and  $t_2$  with and  $t_3$  without dpr, femora slender, no costal spinules, subcostal cell narrow, dark sclerotized,  $r_{2+3}$  very long, bent up to costa at tip, sc complete, tip of anal cell closed by anal cross vein at an right angle, analis long, nearly reaching wing margin, middle of face slightly raised, width of genae equal 4/5 of height of 3<sup>rd</sup> antennal segment, body predominantly shining, its length 3.56 mm ..... sp.n. 153, ?Sciomyzidae
- 88k Mouth opening small, clypeus invisible, vi, pvt convergent, 3+3 pp, 3 sa (posterior weaker); 4-5 strong peristomal bristles, oc divergent, 2-3 ors, 0 m, 4-5 st + 2 smaller setae, prsc, 0 ia, la, ap, sc ends far from  $r_1$ , analis ends at wing margin, axillaris present, body/wing 7.6/6.3 mm ..... sp.n. 154

- 89 (90) Prescutellar (prsc) bristles absent (I, fig. 222). Propleural bristle (pp) absent. Sternopleuron at upper margin with 2 long sternopleural bristles (I, fig. 224). **Costal spinules present, widely separated.** A peculiar basal coastal break outside the humeral crossvein is present. In opposite to HENNIG's description about 8 rows of small acr are present ..... *Electroleria alacris* (MEUNIER), Heleomyzidae
- 89a Without costal spinules,  $f_2$  with a long ventral bristle; vi, 2 ors (anterior shorter), long oc, probably 0 pp, mesopleuron bare, 0 m, 2 st, 2 dc, 0 prsc, 4-5 acr-rows,  $f_1$  in the apical fourth with 1 ventral and 1 dorso-lateral bristle, middle of  $f_2$  with 1 ventral bristle, sc ends as a fold near  $r_1$ , anal cell closed by anal cross vein in an right angle, width of genae below eye equals diameter of 3<sup>rd</sup> (round black) antennal segment, anteriorly broader, palpi thin and yellow, body/wing 3.66/3.02 mm ..... sp.n. 155, ?Sciomyzidae
- 89b All body parts including wings pitch-black (well preserved, 6 *Neottiophilum* syn-inclusions are coloured normal!), clypeus large and well protruding, mesonotum brilliantly shining, only pubescent between dc-lines, space with 6-7 acr-rows, long vi, 2 ors, short pvt, 1 very small pp, mesopleuron bare, 0 m, 2 st, 2 well distant dc, 0 prsc,  $t_3$  with 2 apical short spurs, femora robust, no costal spinules, subcostal break, anal cell closed by anal cross vein in an right angle, width of genae equal diameter of  $f_1$ , surstyli acute, dagger-like, body/wing 3.95/3.46 mm ..... sp.n. 156
- 90 (89) Prescutellar bristles (prsc) present (I, fig. 208, 214). Propleural bristle (pp) long and strong (I, fig. 213). One, two or 3 sternopleural bristles present.
- 91 (92) Mesonotum with 3 pairs of dorso-central bristles present (dc; I, fig. 208). Only one sternopleural bristle present (I, fig. 209). **Anterior ors (of 2) shorter, 1 long pp (I, fig. 147), sternopleuron haired at rear above, 2 dc, costal spinules and dpr on all legs present.** Surely belonging in the genus *Tephrochlamys* LOEW ..... "Heteromyza" *dubia* MEUNIER, Heleomyzidae
- 91a Costal spinules absent, 1 st ..... sp.n. 157
- 91b Costal spinules are present, 2 dc ..... sp.n. 158
- 91c Very similar to "H." *dubia*, with the following differences: sternopleuron only haired in anterior part, in addition to an anterior pp (= proepisternal, in original description called "proepimeral") there occurs a "stigmatal bristle" (= proepimeral of manuals) below the prothoracal spiracle (inserting on the front edge of the mesopleuron), "prescapular" bristles inside of humeral callus missing, the ground-pattern "central cheek bristles" on the postgena (= lower hind edge of the head) absent,  $t_2$  with few ventral setulae, " $f_1$  with a row of nine strong and long bristles anterodorsally", body 3.4 mm ..... *Balticoleria michaeli* WoźNICA, Heleomyzidae
- 91d Subcostal cell is sclerotized and dark,  $r_1$  long, 0 pp, 1 st, some sternopleural hairs, 3 dc ..... sp.n. 159
- 92 (91) Mesonotum with 2 pairs of dorso-central bristles present (I, fig. 214). Three sternopleural bristles present (I, fig. 213) ..... *Chaetohelomyza electrica* HENNIG, Heleomyzidae
- 92a Costal spinules present, soft short hairs on mesopleuron, 1 st, 3rd antennal segment relatively small, short and densely pubescent, body and wing longer than 4 mm ..... sp.n. 160
- 92b Costal spinules absent, mesopleuron bare, 1 st, 2 dc, 3rd antennal segment swollen ..... sp.n. 161
- 92c Costal spinules present, 0 m, 1 st, 2 dc. Go to couplet 91, "H." *dubia*, (dc variability!).

## Family transfers since HENNIG's time

Anthomyzidae, *Anthoclusia gephyrea* HENNIG, 1965 to Neurochaetidae (MCALPINE 1978).

Anthomyzidae, *Anthoclusia remotinervis* HENNIG, 1969 to Neurochaetidae (MCALPINE 1978).

Anthomyzidae, *Xenanthomyza larsoni* HENNIG, 1967 to Clusiidae (MCALPINE 1989).

Calobatidae are used today as Calobatinae, a subfamily of Micropezidae.

Diastatidae, *Pareuthyshaeta minuta* (MEUNIER, 1904) to Campichoetidae (GRIMALDI 2008).

Diastatidae, *Pareuthyshaeta succini* HENNIG, 1965 to Campichoetidae (GRIMALDI 2008).

Lonchaeidae, *Glaesolonchaea electrica* HENNIG, 1967 to Pallopteridae (MORGE 1967).

Lonchaeidae, *Morgea mcalpinei* HENNIG, 1967 to Pallopteridae (MORGE 1967).

**Table 5:** Survey via parts of the studied Acalyptratae with complete scientific names. Material studied by HENNIG included for comparison only, signed with •; E = EICHMANN, G = GRÖHN, Ho = HOFFEINS, K = KERNEGGER, L = LUDWIG, vT = VON TSCHIRNHAUS, T = TEUBER.

<b>Family</b>	<b>Key</b>	<b>Species</b>	<b>•</b>	<b>E</b>	<b>G</b>	<b>Ho</b>	<b>K</b>	<b>L</b>	<b>T</b>	<b>vT</b>	<b>Σ</b>
Acartophthalmidae	30	<i>Acartophthalmites tertaria</i> HENNIG, 1965	5		1	11				3	20
	—	sp.					1				1
Anthomyzidae	47	<i>Protanthomyza collarti</i> HENNIG, 1965	2			4				2	8
	74d	sp.								1	1
Asteiidae	64	<i>Succinasteia carpenteri</i> HENNIG, 1969	1			4				2	7
	64a	<i>Astiosoma</i> sp.								1	1
	25a	sp.				1					1
Aulacigastridae	54	<i>Protaulacigaster electrica</i> HENNIG, 1965	1								1
	6a	sp. 1					1			1	2
	49i	sp. 2								1	1
	54a	sp. 3								2	2
	54b	sp. 4								1	1
Camillidae	51	<i>Protocamilla groehni</i> GRIMALDI, 2008			1						1
	6	<i>Protocamilla succini</i> HENNIG, 1965	7			22				12	41
	—	<i>Protocamilla</i> sp.			1						1
	→	2-3 spp.: partly included in couplets 5b, 5g, 5i				1	2			3	6
Campichoetidae	9	<i>Pareuthyshaeta electrica</i> HENNIG, 1965	11			7	2	1		28	49
	8	<i>Pareuthyshaeta minuta</i> MEUNIER, 1904	1		1	16				7	25
	9a	<i>Pareuthyshaeta</i> sp.								7	7
	5h	sp. 1					1			1	2
Carnidae	56	<i>Meoneurites enigmatica</i> HENNIG, 1965	2							1	3
	56a	<i>Meoneurites</i> sp. 1				1				1	2
	43c	<i>Meoneurites</i> sp. 2								1	1
	42c	sp.					1				1
Chamaemyiidae	77	<i>Procremifania electrica</i> HENNIG, 1965	2	3		3				1	9
	77a	<i>Procremifania</i> sp.			1						1
	40a	sp.		3		2	3			3	11
Chloropidae	32	<i>Protoscinella electrica</i> HENNIG, 1965	1		3	21	5			16	46
	32b	<i>Protoscinella</i> sp.					1			2	3
	72a	<i>Tricimba</i> sp.								1	1
Clusiidae	42	<i>Electroclusiodes meunieri</i> (HENDEL, 1923)	4	1	3	6				17	31
	34	<i>Electroclusiodes radiospinosa</i> HENNIG, 1965	1			3		1	1	1	6
	42b	<i>Electroclusiodes</i> sp. 1								2	2
	42e	<i>Electroclusiodes</i> sp. 2								3	3
	74	<i>Xenanthomyza larssoni</i> HENNIG, 1967	1			1				5	7
	→	9 species: 33b, 42a, 57a, 73a, 74a, 74b, 74c, 74e, 79f		1	2	7	8			15	33
? Clusiidae	—					2					2
Conopidae	2c	<i>Hoffeinsia baltica</i> STUKE, 2005				1					1
	2b	<i>Palaeomyopa hennigi</i> STUKE, 2003									0
	2a	<i>Palaeomyopa tertaria</i> MEUNIER, 1912	2			1					3
	2d	sp.								1	1
Chyromyidae	46	<i>Gephyromyiella electrica</i> HENNIG, 1965	2		3	1					6
	—	sp.				2					2
Cryptochetidae	61	<i>Phanerochaetum tuxeni</i> HENNIG, 1965	2		2	2	2		1	5	14
Cypselosomatidae	66	<i>Cypselosomatites succini</i> HENNIG, 1965	1		1	3	1			1	7
Diopsidae	1	<i>Prosphyracephala succini</i> (LOEW, 1873)	2	1	1	4		1	1		10
	2	sp.					1				1
Drosophilidae	4	<i>Electrophortica succini</i> HENNIG, 1965	1			9	3			6	19
	4b	<i>Electrophortica</i> sp. 1								5	5
	4c	<i>Electrophortica</i> sp. 2								7	7
	—	sp.					1	1			2
Dryomyzidae	85	<i>Palaeotimia lhoesti</i> MEUNIER, 1908	1			1					2
	37	<i>Prodryomyza electrica</i> HENNIG, 1965	2		1	6	1			4	14
	37a	sp.					1			1	2
Heleomyzidae	91c	<i>Balticoleria michaeli</i> WOŹNICA, 2007								1	1
	92	<i>Chaetohelomyza electrica</i> HENNIG, 1965	4			1				1	6
	89	<i>Electroleria alacris</i> (MEUNIER, 1904)	8	2	1	19	12			9	51
	—	? <i>Electroleria</i> sp.			1		6				7
	91,92c	" <i>Heteromyza</i> " <i>dubia</i> MEUNIER, 1904	4	1	2	7	3			9	26

**Table 5:** continued

<b>Family</b>	<b>Key</b>	<b>Species</b>	<b>•</b>	<b>E</b>	<b>G</b>	<b>Ho</b>	<b>K</b>	<b>L</b>	<b>T</b>	<b>vT</b>	<b>Σ</b>
	19d	<i>Paleohelomyza kotejai</i> Woźnica & Palaczyk, 2005				1				1	2
	16n	<i>Protoorbellia hoffeinsorum</i> Woźnica, 2006				2					2
	19	<i>Protosuillia media</i> (Meunier, 1904)	4			2	2			5	13
	18	<i>Suillia major</i> Meunier, 1904	4		8	18	7	7		16	60
	—	Heleomyzinae species				2					2
	—	Suilliinae species				20	2				22
	→	sp. 16f, 42k, 88e				3	8			5	16
? Heleomyzidae	—					3					3
Lauxaniidae	87	<i>Chamaelauxania succini</i> Hennig, 1965	3		1	3	1			10	18
	—	<i>Chamaelauxania</i> sp.				3					3
	44	<i>Hemilauxania incurviseta</i> Hennig, 1965	2		1	5	3			6	17
	—	<i>Hemilauxania</i> sp.				2					2
	→	species (partly to be included in couplet 79c)		1	1	6	2			3	13
Megamerinidae	24	<i>Palaeotanypeza spinosa</i> Meunier, 1917	1		1	4				2	8
	—	sp.				1					1
Micropezidae	69	<i>Electrobata tertaria</i> Meunier, 1909	4		1	7				2	14
	68	<i>Electrobata myrmecia</i> Hennig, 1965	2			1				1	4
	68a	<i>Electrobata</i> sp. 1								1	1
	68b	<i>Electrobata</i> sp. 2								1	1
	68c	<i>Electrobata</i> sp. 3				1					1
	75a	sp. 1								1	1
	—	sp.	1			1					2
Milichiidae	52a	<i>Phylloomyza jaegeri</i> Hennig, 1967	2			9	2	1		2	16
	52b	<i>Pseudodesmometa succineum</i> Hennig, 1971	1							2	3
	52c	<i>Pseudodesmometa</i> sp.								2	2
	→	sp. (partly to be included in couplet 52d)				11				1	12
Natalimyzidae	4a	<i>Natalimyza</i> sp.				1				1	2
Neurochaetidae	58,73	<i>Anthoclesia gephycra</i> Hennig, 1965	2		2	4				2	10
	59	<i>Anthoclesia remotinervis</i> Hennig, 1969	1			5				1	7
	—	sp.				5					5
Odiniidae	15	<i>Protodinia electrica</i> Hennig, 1965	1		3	8	1			7	20
	—	sp.				1					1
Pallopteridae	16	<i>Pallopterites electrica</i> Hennig, 1967	1			4		1		3	9
	40	<i>Glaesolonchaea electrica</i> Hennig, 1965	2			4	3			5	14
	49	<i>Morgea mcalpinei</i> Hennig, 1967	1			3	1			5	10
	49e	<i>Morgea</i> sp.								2	2
	16a	sp.				2	1			4	7
Periscelididae	5k	<i>Procyamops succini</i> Hoffeins & Rung, 2005				1					1
	24a	sp. 1								2	2
	49c	sp. 2								2	2
Proneottiophilidae	14	<i>Proneottiophilum extinctum</i> Hennig, 1969	1			11				12	24
	14b	<i>Proneottiophilum</i> sp. 1				1				2	3
	48a	<i>Proneottiophilum</i> sp. 2								2	2
Pseudopomyzidae	17a	<i>Eopseudopomyza kuehnei</i> Hennig, 1971	1		1	8	2			7	19
	—	sp.				4					4
Psilidae	25	<i>Electrochyliza succini</i> Hennig, 1965	7	1	1	10				15	34
	—	sp.			1		1	1			3
Pyrgotidae	43a	sp. 1					1				1
	45b	sp. 2					1				1
Sciomyzidae	36	<i>Prophaeomyia loewi</i> Hennig, 1965	4			7	3	1		1	16
	84	<i>Palaeoheteromyza curticornis</i> Hennig, 1965	3								3
	80	<i>Prosalticella succini</i> Hennig, 1965	2		3	9				1	15
	21	<i>Palaeoheteromyza crassicornis</i> Meunier, 1904	2			3					3
	82	<i>Palaeoheteromyza investiganda</i> Hennig, 1965	1			2					3
	76	<i>Sepedonites baltica</i> Hennig, 1965	2			1					3
	→	spp. 16b 21a 36a 42f 49a 49d 49h 76a 80a 85b 88i 89a				4	21	3		24	52
? Sciomyzidae	—	not considered in the key					7				7
Sepsidae	29	<i>Protorygma electricum</i> Hennig, 1965	1			3					4
familiae inc. sed.	→	sp. 1 & sp. 2: couplets 19h and 40f				2					2
familiae inc. sed.		many different couplets, some without couplets	0	8	3	48	3	0	0	141	203
Sum of included Acalyptratae (at least 217 species: 56 valid taxa, 161 new species)			124	24	57	465	86	13	2	491	1262

## Outlook

Our overview and provisional identification key is only thought to be a first step for a continuation of amber studies. Working with Diptera in amber will raise more questions than can be responded satisfactorily. The authors invite specialists from all over the world to follow the footprints of Hermann LOEW, Fernand MEUNIER and Willi HENNIG. We promise you will need steadiness but will enjoy it!

## Zusammenfassung

Eine Zusammenstellung der 38 Veröffentlichungen, die sich mit Diptera Acalyptratae aus dem Baltischen Bernstein beschäftigen, umfasst den Zeitraum 1822 bis 2008. H. LOEW war der erste Entomologe, der systematisch nach Bernstein-Dipteren suchte. Zwei seiner drei diesbezüglichen Arbeiten werden diskutiert, Abschnitte aus der ersten (1850) wegen der extremen Seltenheit der Publikation in öffentlichen Bibliotheken ins Englische übersetzt. Heute sind 35 Familien der Acalyptratae aus dem baltischen Eozän bekannt, drei weitere aus Eozän-Sedimenten Englands. Erstmals werden hier Natalimyzidae, ?Piophilidae und Pyrgotidae nachgewiesen, *Natalimyza* war bisher nur rezent aus der Afrotropis bekannt. Unterschiedliche Zählungen des prozentualen Anteils von Acalyptratae unter allen Insekten, allen Dipteren und allen Fliegen werden miteinander verglichen. Weniger als 1% aller Fliegen erweisen sich als Acalyptratae. Gründe für deren Seltenheit werden zusammen mit einer Übersicht über seltene Aggregationen mehrerer Fliegen in einem einzelnen Inklusenstein diskutiert. Morphologische Apomorphien, die wegen ihrer Einmaligkeit rezente Fliegenfamilien weltweit erkennen lassen, waren bereits im Tertiär evolviert. Der Disput über die angezweifelte synchrone Entstehung des deutschen Bitterfelder Bernsteins kann hier aufgrund von 15 Arten entschieden werden, die identisch in beiden Bernsteinlagerstätten vorkommen. Niemals zuvor wurde die intraspezifische Variabilität an Bernstein-Acalyptratae studiert. An einer Serie von 45 Exemplaren und dem Holotypus der Halmfliege *Protoscinella electrica* (Chloropidae) werden die evolutionären Transformationen von 16 ausgewählten Merkmalen während einer Zeitspanne von 10 Millionen Jahren exemplifiziert unter Berücksichtigung des phylogenetischen Wertes dieser morphologischen Details. Daraus ergibt sich ein kleiner Einblick auf den polyphyletischen Reduktionsprozess bestimmter Flügeladern und Borstenausstattungen bei verschiedenen Familien der Acalyptratae.

Der systematische Teil der Arbeit präsentiert Über-sichten über eine große Anzahl morphologischer De-

tails, die für die Taxonomie von Acalyptratae benutzt werden. Zwei Tabellen erleichtern die Protokollarbeit bei Inklusenuntersuchungen sowie das leichtere Verständnis der verwirrenden Fachtermini und Abkürzungssysteme in aufeinander folgenden Perioden der Dipterologie. Zwei unterschiedlich gestaltete Bestimmungsschlüssel werden präsentiert, einer nach 97 außergewöhnlichen, seltenen oder neu entdeckten morphologischen Besonderheiten, ein zweiter ist der Versuch, alle 56 beschriebenen und alle 161 neu entdeckten Arten zu erkennen. Die Schlüssel legen bewusst die altbekannte Terminologie zugrunde, die HENNIG in seinen Bernstein-Publikationen verwendete und ermöglichen so den Quervergleich zu seinen zahlreichen komplizierten Beschreibungen und den vielen Abbildungen, ebenso zu den lange eingebürgerten Termini in der dipterologischen Literatur bis 1981, dem Jahr, in welchem neue Termini kreiert wurden. Alle Familien- und Gattungs-Transfers seit HENNIGS Zeit werden mit ihren Quellen aufgelistet, ergänzt durch eine Arten-Übersicht über einen Teil der 1.141 zusammengetragenen Acalyptratae-Inklusen.

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